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The Ordovician graptolites of the Shelve District, Shropshire

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Synopsis

The distribution of graptolites in the Ordovician of the Shelve area is recorded, based largely on the collections made for the late Professor W. F. Whittard in the 1950s and 1960s while he was mapping the area and monographing the trilobites. This is the first illustrated account of the comparatively poor graptolite faunas. Some 60 species are here described but no new names are proposed. A lectotype of *Leptograptus latus* Elles & Wood 1903 is selected. Almost every species requires critical re-examination of types (almost entirely from other areas) and population studies which cannot be done on the existing material.

The Ordovician of Shelve, from Arenig to basal Caradoc, is probably the most complete for this span of time in the British Isles and with this contribution the macrofauna is largely described, so that detailed comparison with other areas is now possible.

Introduction

Graptolites were first recorded from the Shelve Inlier in Murchison's *Silurian System* (1839), in which he described the new species *Graptolithus foliaceus* from the Meadowtown beds. Subsequent records have been sporadic and although there were further records in the 19th century there was no description of specimens from Shelve until the first part of Elles & Wood's monograph in 1901. Morton (1877), Lapworth (1879, 1887) and particularly Lapworth & Watts (1894) provided some species names associated with a few localities, and by 1890 Lapworth had certainly collected fairly systematically from the most fossiliferous levels. The Shelve Church Beds were well known by 1875 for the abundance of dendroids to be found there. With the publication of the first few parts of Elles & Wood's monograph, illustrations of Shelve species appeared in some numbers and in the text there were further records of the species to be found in the inlier. In 1892, Lapworth had managed to persuade the Geological Survey to let John Rhodes collect from selected horizons in both the Shelve and Caradoc/Wrekin areas so that representative Cambrian and Ordovician faunas could be assembled; a second collecting foray, this time by Manson, was undertaken in 1914. Lapworth provided a report based on these, and vertical sections of the strata, in 1916. There are few additional records of graptolites in the later accounts (summarized by Whittard, 1931) and it was generally assumed that the lithological sequence proposed by Lapworth was well known and dated. When, in the early 1950s, Whittard found that in places the stratigraphy was more complicated than shown on the small-scale map of Lapworth & Watts (1894), he wanted someone to identify the graptolites, as they were found, to tie his trilobite work into the standard succession of zones. At O. M .B. Bulman's suggestion, I undertook this task in 1955 and at various times during the next ten years I had parcels of specimens, with only locality numbers, to identify. One of the first surprises was the recognition that the highest beds in the inlier were much lower stratigraphically than had been previously suggested. With Whittard's sudden death in 1966, the Shelve material was left until the stratigraphical framework had been published (Whittard, ed. Dean 1979), but in the meantime there had been a very great increase in worldwide publications on Ordovician graptolites, particularly in Russia and latterly in China. It has not been possible to re-examine all the Whittard Collection but representative specimens from different horizons and localities have been restudied. With the trilobites (Whittard 1955–67) and the brachiopods (Williams 1974) now monographed and the map (Whittard, ed. Dean 1979) available, the third main group of fossils is illustrated here.

The graptolites are found in a wide variety of lithologies, from black micaceous silty shales to impure sandy limestones and volcanic ashes. They are only rarely found as the silvery films characteristic of true graptolitic shales and photography of black specimens on dark rocks has proved difficult. In the Rorrington and Aldress Members, which are the richest in variety of forms, the graptolites are frequently pyritized but retain their black skeleton. Weathered specimens, however, can provide a good colour contrast for photography. Line drawings have been made of specimens which it was impossible to photograph satisfactorily. The plates have been arranged stratigraphically so that a general view of the faunas at different horizons can be easily obtained.

Table 1 Stratigraphical distribution of species arranged in order of appearance.

	Mytton	Hope	Stapeley	Weston	Betton	Meadowtown	Rorrington	Spy Wood	Aldress	Hagley	Whittery
Clonograptus sp.	+	–	–	–	–	–	–	–	–	–	–
Tetragraptus cf. *bigsbyi*	+	–	–	–	–	–	–	–	–	–	–
?*Tetragraptus* sp.	+	–	–	–	–	–	–	–	–	–	–
Expansograptus cf. *hirundo*	+	–	–	–	–	–	–	–	–	–	–
E. cf. *nitidus*	+	–	–	–	–	–	–	–	–	–	–
E. cf. *praenuntius*	+	–	–	–	–	–	–	–	–	–	–
E. cf. *simulans*	+	–	–	–	–	–	–	–	–	–	–
E. cf. *sparsus*	+	–	–	–	–	–	–	–	–	–	–
E. cf. *suecicus*	+	–	–	–	–	–	–	–	–	–	–
Corymbograptus deflexus	+	–	–	–	–	–	–	–	–	–	–
C. cf. *inflexus*	+	–	–	–	–	–	–	–	–	–	–
Isograptus sp.	?	–	–	–	–	–	–	–	–	–	–
Glyptograptus dentatus	?	+	–	–	–	–	–	–	–	–	–
G. shelvensis	+	–	–	–	–	–	–	–	–	–	–
Pseudophyllograptus cf. *angustifolius*	–	+	–	–	–	–	–	–	–	–	–
P.(?) cf. *glossograptoides*	–	+	–	–	–	–	–	–	–	–	–
Didymograptus pluto	–	+	+	–	–	–	–	–	–	–	–
D. cf. *stabilis*	–	+	+	–	+	–	–	–	–	–	–
Expansograptus cf. *euodus*	–	+	–	–	–	–	–	–	–	–	–
Acrograptus acutidens	–	+	–	–	–	–	–	–	–	–	–
A. gracilis	–	+	–	–	–	–	–	–	–	–	–
Glossograptus cf. *armatus*	–	+	–	–	–	–	–	–	–	–	–
Amplexograptus cf. *confertus*	–	?	?	–	–	–	–	–	–	–	–
Glyptograptus sp.	–	+	–	–	–	–	–	–	–	–	–
Didymograptus aff. *miserabilis*	–	–	+	–	+	–	–	–	–	–	–
Glossograptus cf. *acanthus*	–	–	+	–	–	–	–	–	–	–	–
G. fimbriatus	–	–	+	–	–	–	–	–	–	–	–
Didymograptus murchisoni	–	–	–	+	+	–	–	–	–	–	–
Gymnograptus (?) sp.	–	–	–	–	+	–	–	–	–	–	–
Cryptograptus schaeferi	–	–	–	–	–	+	–	–	–	–	–
Dicellograptus divaricatus	–	–	–	–	–	+	+	–	–	–	–
D. sextans	–	–	–	–	–	?	+	–	–	–	–
D. cf. *vagus*	–	–	–	–	–	+	–	–	–	–	–
Dicranograptus irregularis	–	–	–	–	–	+	–	–	–	–	–
D. sp.	–	–	–	–	–	+	–	–	–	–	–
Diplograptus foliaceus	–	–	–	–	–	+	–	–	+	+	+
Climacograptus aff. *antiquus lineatus*	–	–	–	–	–	+	+	–	+	+	–
Nemagraptus gracilis	–	–	–	–	–	–	+	–	–	–	–
N. gracilis cf. *distans*	–	–	–	–	–	–	+	–	–	–	–
Leptograptus validus	–	–	–	–	–	–	+	–	–	–	–
L. latus	–	–	–	–	–	–	+	–	–	–	–
Dicellograptus intortus	–	–	–	–	–	–	+	+	–	–	–
D. salopiensis	–	–	–	–	–	–	+	–	–	–	–
D. exilis	–	–	–	–	–	–	+	+	–	–	–
Dicranograptus brevicaulis	–	–	–	–	–	–	+	–	–	–	–
D. rectus	–	–	–	–	–	–	+	+	–	–	–
Diplograptus leptotheca	–	–	–	–	–	–	+	–	+	+	+
Glyptograptus teretiusculus	–	–	–	–	–	–	+	–	–	–	–
Orthograptus uplandicus	–	–	–	–	–	–	+	+	–	–	–

Table continued over

Table 1 continued.

	Mytton	Hope	Stapeley	Weston	Betton	Meadowtown	Rorrington	Spy Wood	Aldress	Hagley	Whittery
Climacograptus brevis	–	–	–	–	–	–	+	–	+	–	–
Pseudoclimacograptus modestus	–	–	–	–	–	–	+	–	–	–	?
Orthograptus cf. *apiculatus*	–	–	–	–	–	–	–	+	+	–	–
Cryptograptus tricornis	–	–	–	–	–	–	–	–	+	–	–
Corynoides cf. *curtus*	–	–	–	–	–	–	–	–	+	–	–
Diplograptus multidens	–	–	–	–	–	–	–	–	+	–	–
Amplexograptus fallax	–	–	–	–	–	–	–	–	+	–	–
Orthograptus truncatus	–	–	–	–	–	–	–	–	+	–	+
Climacograptus sp.	–	–	–	–	–	–	–	–	+	–	–
C. cf. *tubularis*	–	–	–	–	–	–	–	–	+	–	–
Lasiograptus costatus	–	–	–	–	–	–	–	–	+	–	–
Climacograptus peltifer	–	–	–	–	–	–	–	–	–	+	–
Pseudoclimacograptus scharenbergi	–	–	–	–	–	–	–	–	–	+	+

Whittard's graptolite material on which this study is based is all now preserved in the Department of Palaeontology, British Museum (Natural History); register numbers are prefixed by Q. Other material, prefixed BU, in Birmingham University Museum, GSM, in British Geological Survey, and SM, in Sedgwick Museum, Cambridge.

Faunal succession

Mytton Member. Most of the 25 localities have only one or two species present, and although some dozen species are found overall it is not possible to say more than that the fauna is Arenig in age. The most widespread species is *E. nitidus* which is found in five different localities, and in the absence of good specimens of *E. hirundo* it is most likely that the greater part of the Mytton Member should be referred to the *extensus* Zone of the old nomenclature. The status of subdivisions of this zone, as well as a critical re-examination of a *hirundo* Zone as such, needs much further collecting and study in Britain. At one time, the topmost beds of the Mytton Member were separated off as the Tankerville Flags. Bergam Quarry (Loc. 783) has yielded *E.* cf. *suecicus* as well as *E. nitidus*, which provides a link to the overlying '*bifidus*' Zone from which it has been more usually recorded. No pendent didymograptids have been found so far in the Mytton Member. Records of *E. hirundo* have almost all been of single, broad dichograptid stipes which could be tetragraptid. There is a single isograptid which occurs without associates and appears to be a new species.

Hope Member. There are some 50 localities in this unit yielding graptolites but in about half of them the specimens are fragmentary or only identifiable as *Didymograptus* sp. A problem in the first identifications of the collection was that forms referable to both *D.* '*bifidus*' and *D. murchisoni* occurred in the Hope Member. The association with *A. acutidens* and *A. gracilis*, however, strongly suggests the lower part of the Llanvirn for this member. It is unfortunate that only single specimens of the phyllograptoids have been found so that their identification is uncertain, as they might have provided some better control by comparison with Scandinavia. Not all the localities have been found in Whittard's notes and no attempt has been made to compare the faunas of beds below and above the Chinastone Ash which has been used as a field division into upper and lower parts of the member. Few localities have more than two or three recognizable species present and there is no obvious grouping of localities by fauna.

Stapeley Volcanic Member. There are only three graptolite localities in this member amongst the material which I have seen. One of these yielded *Glyptograptus* sp., another indeterminate slender dichograptid stipes and the third pendent didymograptids. The horizon cannot be more precisely placed than Llanvirn.

Stapeley Shale Member. This, as might be expected, is considerably more fossiliferous than the underlying volcanic member but few localities have more than one species present. The richest locality has *A. acutidens*, *D. pluto* and *G. fimbriatus*, which clearly puts it in the lower part of the Llanvirn. Other species which occur in the member include *D. stabilis*, *D. miserabilis* and *Amplexograptus confertus*, providing links mainly with the earlier Hope Member. Loc. 463, which has *D. miserabilis*, is close to the base of the succeeding Weston Member.

Weston Member. There are only a few graptolitic localities in this member and originally Whittard (1955: 5) put the Weston Beds in the *bifidus* Zone. The pendent didymograptids appear to belong to *D. murchisoni*, which suggests association with the overlying Betton Member which is clearly of *D. murchisoni* age. The trilobites apparently support this interpretation (Whittard 1966: 297). The preservation of the graptolites is usually poor.

Betton Member. The shales of this unit are characterized by the abundance of large pendent didymograptids, generally assigned to *D. murchisoni*. There are a few other forms of *Didymograptus* present and a number of localities have *Gymnograptus*(?) sp. The specimens are often distorted by cleavage and it has not been possible to undertake any detailed analysis of the forms present. This doubtful record of *Gymnograptus* suggests correlation with the comparable beds in Scandinavia where *G. linnarssoni* occurs in the beds overlying the Upper Didymograptus Shale. One of the localities for this form is put just on the boundary of the Betton and Meadowtown Members on the revised map (Whittard, ed. Dean 1979: 44, fig. 30), but the biserial forms are accompanied by *D.* cf. *murchisoni* while Hede (1951) does not record *G. linnarssoni* even in his transition beds between the *D. clavulus* and *G. linnarssoni* Zones. The difficulties in comparing the records of *Gymnograptus* from different countries are discussed on p. 46.

Meadowtown Member. In a letter to me of 3/10/55, Whittard commented of the Meadowtown Member that 'both top and bottom junctions are gradational'. He sent me several samples with the request that I decide whether they should be placed in it on the graptolite evidence alone, since at that time the *D. murchisoni* Zone below and *N. gracilis* Zone above were considered easily recognizable. Unfortunately not only are the beds generally lithologically distinct, with a rich shelly fauna in places, but the graptolites are comparatively restricted in variety: they consist largely of long-ranging forms of diplograptids whose comparative taxonomy is poorly known. Meadowtown Quarry is the type locality for *Diplograptus foliaceus* (Murchison), a species name which, as Elles & Wood noted in 1908, had been used for a wide range of different forms. It is still not possible to define its range adequately, since very similar forms are found in all the coarser units in the Shelve Inlier above the Meadowtown Member, right up to the Whittery Member at the top. They do not appear, however, in the immediately overlying shaly Rorrington Member, where a much wider range of diplograptids is found. This may reflect some change in source area; I do not think there is any good evidence for ecological control of distribution such as depth of water. The Meadowtown Member has generally been correlated with the zone of *Glyptograptus teretiusculus* by default, there being no pendent didymograptids to put it with the *murchisoni* Zone below nor nemagraptids to associate it with *N. gracilis* Zone above. The reality of the *teretiusculus* Zone has been a matter of debate for many years and the Shelve area provides little evidence to help. *Dicellograptus* sp. occurs at Loc. 164 just west of Meadowtown Quarry, about the middle of the member, while *Dicranograptus irregularis* occurs further south at a lower horizon along with *Dicellograptus vagus*. These two Swedish species were originally described from the *C. putillus* Zone and this suggests that there is something recognizable between the *murchisoni* and *gracilis* Zones.

Rorrington Member. The dark shales of the Rorrington Member have long provided beautiful specimens of graptolites, often in full or partial relief but difficult to study in comparison with the more usual silvery films of thin graptolitic sequences. Over 50 localities provide some 20 species, usually in abundance on the slabs. Lapworth (1916) divided the shales into successive *Nemagraptus* Beds and *Leptograptus* Beds and noted a *Dictyonema* horizon. There is material from a number of Whittard's localities which yields dendroids, but in the Spy Wood Brook section they cover both middle and upper parts of the Rorrington Member; there is thus not just a single recognizable horizon. The division into *Nemagraptus* and *Leptograptus* Beds seems to have been based on Manson's collecting in the stream section south of Desert (Whittard, ed. Dean 1979: 42, fig. 28) and to some extent in Holywell Brook near Rorrington. I have been unable to trace all of Whittard's localities so it is not yet possible to confirm the sequence. However, amongst the Rorrington localities there are 10 yielding *Nemagraptus* but no *Leptograptus*, 8 with *Leptograptus* but no *Nemagraptus* and 9 with both genera. Many of the localities are in the Spy Wood Burn area where Whittard's map shows some complicated faulting, but there are suggestions that locally *Nemagraptus* Beds occur below *Leptograptus* Beds. The rest of the fauna includes *Dicranograptus brevicaulis*, *D. rectus*, *Dicellograptus sextans*, *D. salopiensis*, *D. divaricatus*, *D. intortus*, various climacograptids and rarer orthograptids. Many of these are also found in the overlying Spy Wood Member. There is no doubt that this represents a typical *N. gracilis* Zone assemblage and it is unfortunate that the members below and above have such a different lithology that the succession of faunas is obscured by facies-imposed differences.

Spy Wood Member. There are about a dozen localities in this basically sandy member which yield graptolites, but generally they have only two or three species each so that proper zonal consideration is not possible. Dicellograptids and dicranograptids continue from the Rorrington Member, as do various diplograptids, but there are no *Leptograptus* or *Nemagraptus*. The latter, however, is found in the beds near Rorrington Hall which were labelled 'passage beds from Rorrington to Spy Wood', so it is possible that the absence of *Nemagraptus* is simply the result of different facies. This is important since high Costonian trilobites have been recorded from the Spy Wood Member, suggesting that some at least of the basal Caradocian is to be assigned to the *N. gracilis* Zone. *Orthograptus uplandicus* is the most widespread species in this member but it also occurs in the Rorrington Member and possibly in the Aldress Member, so that it is not a great deal of use stratigraphically.

Aldress Member. There are several species which are found only in this unit, such as *Lasiograptus costatus*, *Dicranograptus ramosus spinifer* and *Corynoides*, but apart from the first of these they are all very rare and do not greatly help stratigraphically. Elles & Wood (1908) record *L. costatus* from *gracilis* to *wilsoni* Zones and there are only a few records from outside Britain, none of which agree with the British material. In the absence of *Nemagraptus*, *Dicellograptus* and *Leptograptus*, it is tempting to assume that the Aldress Member cannot be in the *gracilis* Zone, but there is as yet no detailed account available of the ranges of species in Britain in this part of the geological column. The Builth succession apparently does not go above the *gracilis* Zone and the succession in the Dicranograptus Shales of south Wales shows considerable differences particularly the occurrence of *Dicellograptus* spp. and *Dicranograptus* spp. in the *arctus* Beds and *Mesograptus* Beds which are the most likely equivalents of the Aldress Member (Strahan *et al.* 1914).

Hagley Volcanic Member. There are only a few localities of this unit in the Whittard Collection from which he sent me graptolites. The initial indication was of a horizon much lower than had been generally accepted. Re-examination of the specimens in the Survey collection identified by Miss Elles showed the presence of a single specimen of *Climacograptus peltifer*, suggesting a low Caradoc horizon which agreed with the trilobite evidence. The rest of the fauna consists of other climacograptids and probably some orthograptids. It has been common practice to refer these to a *D. multidens* Zone which is post-*gracilis* and pre-*clingani*, but the term is unfortunate as *D. multidens* seems to be virtually confined to its type area at Pontesford and only a single

specimen appears in the Whittard Collection from the Aldress Member. Many records of *D. multidens*, based on thecal count, are in fact *D. foliaceus* which has a long range in Shelve from Meadowtown to Whittery Shale Members. However, until a revision of the ranges of the various diplograptids in this part of the Ordovician is available, the subdivision of the graptolitic sequence remains uncertain.

Hagley Shale, Whittery Volcanic and Whittery Shale Members. These all have virtually the same fauna, consisting of biserial forms, *Climacograptus*, *Pseudoclimacograptus*, *Diplograptus* and *Orthograptus*. Most of the species are also found in the Aldress Member and it is difficult to know how much higher than the *gracilis* Zone the succession goes. I would prefer to keep them in the *C. peltifer* Zone but the total absence of *Dicellograptus* and *Dicranograptus* limits comparisons with areas such as south Wales and southern Scotland.

Systematic descriptions

Order **DENDROIDEA** Nicholson, 1872

Family **ANISOGRAPTIDAE** Bulman, 1950

Genus ***CLONOGRAPTUS*** Hall, 1873

TYPE SPECIES. *Graptolithus rigidus* Hall 1858.

Clonograptus sp.
Fig. 1; Pl. 1, fig. 11

DESCRIPTION. Rhabdosome apparently much branched, stipes 0·7 mm wide with simple thecae about 1 mm long; no trace of bithecae.

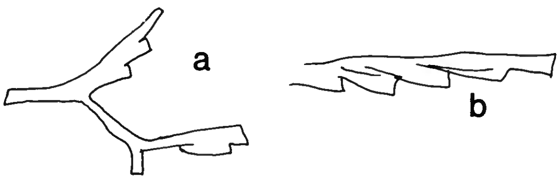

Fig. 1 *Clonograptus* sp. Q.5201, Loc. 933. a, detail of branching; b, distal thecae. Both × 10.

DISCUSSION. A single occurrence (Q.5201) is represented by crowded stipes in relief but some fragments are missing between the part and counterpart so that it is not possible to sort out the tangle of stipes. There are no indications of any sicular portions by thickening but it is possible that several rhabdosomes are present, as there are a number of places where the branching could be interpreted as initial. The length of these straight portions is only 1 mm, however, which suggests rather that they represent consecutive dichotomies in progressive branching at high angles, 90°–120°. There are no long distal stipes. Monsen (1937) gives the length of branching stipes in *C.* cf. *flexilis* (Hall) as 1–1·2 mm but this is about half the length given by Hall (1865) and Ruedemann (1947) gives 3–10 mm for the stipe length.

MATERIAL AND HORIZON. The specimen is from beds mapped as Mytton Member by Whittard (Loc. 933) and is associated with some other dendroids (Q.5202) and a few broad (2·0–2·4 mm) dichograptid stipe fragments (Q.5203).

Order **GRAPTOLOIDEA** Lapworth, 1875

Family **DICHOGRAPTIDAE** Lapworth, 1873

Subfamily **DICHOGRAPTINAE** Lapworth, 1873

Genus ***TETRAGRAPTUS*** Salter, 1863

TYPE SPECIES. *Fucoides serra* Brongniart 1828.

Tetragraptus cf. *bigsbyi* (Hall 1865)
Fig. 2

cf. 1965 *Tetragraptus bigsbyi* (Hall); Skevington: 4; text-figs 1, 3, 5, 6 (with synonymy and discussion).

DISCUSSION. A single specimen from Shelve shows the recurved stipes characteristic of this species, but only two stipes are visible. Since it is clearly not an isograptid, it is presumed to be a tetragraptid and agrees well with this species group. Details of the proximal end cannot be determined as the counterparts are broken and it is possible that this is a fragment with only two stipes; the matrix is a fairly coarse silt. The better-preserved stipe matches fairly well with the lectotype as figured by Skevington (1965), but is less curved and the thecae may not be fully developed since the width of the stipe is much less (2·4 mm instead of 3·1 mm). In this, the specimen is close to var. *divergens* Monsen 1937, as also in the number of the thecae (15–16 per cm), but the shape of the proximal end does not agree with the Norwegian form. Since the specimen is incomplete, it seems best to leave the identification fairly open.

MATERIAL AND HORIZON. The specimen (Q.5204) is associated with the proximal end of a didymograptid (Q.5205), specifically indeterminate, and is from the Mytton Member (Loc. 779).

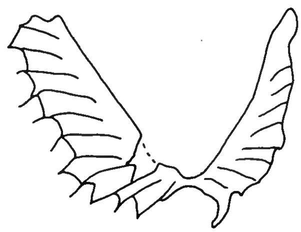

Fig. 2 *Tetragraptus* cf. *bigsbyi* (Hall). Q.5204, Loc. 779. × 5.

?*Tetragraptus* sp.
Pl. 1, fig. 13

A single specimen (Q.5206) occurs alone at Loc. 279 (Whittard, ed. Dean 1979: 19) and consists apparently of two reclined stipes arising from a rather square axil. The longer stipe is 28 mm long and reaches a width of 1·6 mm, with 10 thecae per cm. Close examination suggests that

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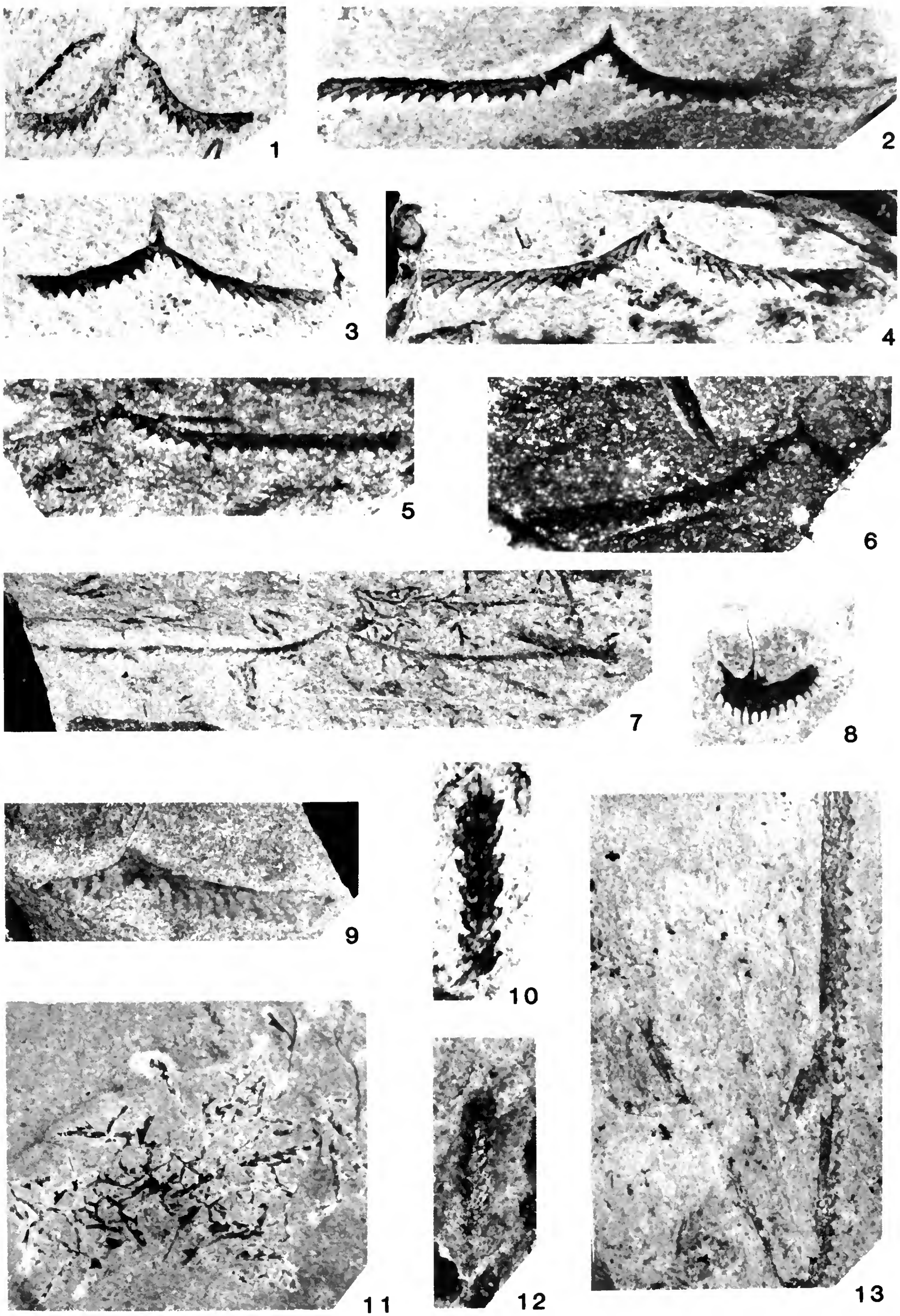
PLATE 1 All specimens from the Mytton Member.

Fig. 1 *Corymbograptus deflexus* (Elles & Wood), p. 20. Q.5246, Loc. 720[1]. × 3. See also Text-fig. 11, p. 20.
Figs 2–5 *Expansograptus* cf. *nitidus* (Hall), p. 18. Fig. 2, Q.5235, Loc. 720[2]. Fig. 3, Q.5236, Loc. 720[1]. Fig. 4, Q.5237, Loc. 720[7]. Fig. 5, BU.2074 (J. T. Wattison collection), Shelve Church. All × 3.
Fig. 6 *Corymbograptus* cf. *inflexus* (Chen & Xia, *in* Mu *et al.* 1979), p. 21. BU.2075, Shelve Church. × 3. See also Text-fig. 12, p. 21.
Fig. 7 *Expansograptus* cf. *simulans* (Elles & Wood), p. 19. Q.5242, Loc. 905. × 2.
Fig. 8 *Isograptus* sp., p. 21. Q.5247, Loc. 791. × 3. See also Text-fig. 13, p. 22.
Fig. 9 *Expansograptus* cf. *hirundo* (Salter), p. 18. Q.5234, Rhodes Locality (Tankerville Flags). × 3.
Fig. 10 *Glyptograptus shelvensis* Bulman, p. 38. BU.2076, Shelve Church. × 6.
Fig. 11 *Clonograptus* sp., p. 7. Q.5201, Loc. 933. × 3.
Fig. 12 *Glyptograptus dentatus* (Brongniart), p. 37. Q.5307, Loc. 905. × 3. See also Pl. 2.
Fig. 13 ? *Tetragraptus* sp., above. Q.5206, Loc. 279. × 3.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there may be a second pair of stipes superimposed on the obvious one; the whole structure looks much more like a reclined tetragraptid than a distorted didymograptid. The stipes, however, are much narrower than most of the described species of *Tetragraptus*. The small species described from China (Geh 1964, etc.) have only short stipes which are also curved.

Genus *PSEUDOPHYLLOGRAPTUS* Cooper & Fortey, 1982

TYPE SPECIES. *Phyllograptus angustifolius* Hall 1858.

***Pseudophyllograptus* cf. *angustifolius* (Hall 1858)**
Fig. 3; Pl. 2, fig. 1

cf. 1858 *Phyllograptus angustifolius* Hall: 139.
cf. 1982 *Pseudophyllograptus angustifolius angustifolius* (Hall) Cooper & Fortey: 242; text-figs 48e, f (with synonymy).

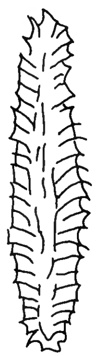


Fig. 3 *Pseudophyllograptus* cf. *angustifolius* (Hall). Q.5207b, Loc. 635. Counterpart of Pl. 2, fig. 1, ×2½.

A single specimen (Q.5207) has been found among the Shelve material which matches most of the descriptions of this widespread species. It is 18 mm long and has a maximum width of 4 mm, which is attained in the first 10 mm of growth, and the rhabdosome tapers distally. The thecae are simple tubes, highly inclined to the length of the rhabdosome and number 7 in the first 5 mm, reducing to 6 in 5 mm distally. They bear short ventral projections. The specimen is not well preserved but appears to show the lateral view of two stipes with only traces of the central series being indicated proximally. It is from the Hope Member, Loc. 635.

***Pseudophyllograptus*(?) cf. *glossograptoides* (Ekström 1937)**
Fig. 4; Pl. 2, fig. 2

cf. 1937 *Phyllograptus glossograptoides* Ekström: 35; pl. 6, figs 26–33.

Another single specimen (Q.5208) from the Hope Member (Loc. 922) also shows the characteristic phyllograptoid thecal arrangement proximally, but it is shorter and wider than the previously described specimen. It is only 10 mm long but reaches a width of 4·8 mm in the first few mm which is then maintained throughout. The thecae number 12 per cm and bear well-developed ventral processes which Ekström (1937) regarded as characteristic of his species. In the absence of a good proximal end, it is not possible to decide whether Ekström's species should be put into *Pseudophyllograptus* or retained in the rarer genus *Phyllograptus*. It has no associates.

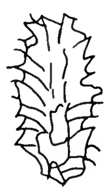


Fig. 4 *Pseudophyllograptus* (?) cf. *glosso-graptoides* (Ekström). Q.5208, Loc. 922. Drawing of Pl. 2, fig. 2, ×2½.

Genus *DIDYMOGRAPTUS* M'Coy, 1851

TYPE SPECIES. *Graptolithus Murchisoni* Beck 1839.

The genus *Didymograptus* is here restricted to pendent forms and the classification of other two-stiped forms is discussed on p. 15 under *Expansograptus*. Skevington (1973) has briefly discussed the difficulties in assigning pendent didymograptids to species and Cooper & Fortey (1982) have also considered the problem. Bouček (1973) concluded that the type of proximal end development was a clear specific character in forms which were otherwise homoeomorphic and Cooper & Fortey have raised this character to subgeneric rank. Unfortunately it is not possible to tell in many cases whether $th1^1$ or $th1^2$ is the dicalycal theca even in the partially three-dimensional material from Shelve, and the critical identification of specimens on this character is not possible. There are very few localities in the Shelve area which provide young specimens and there is extensive proximal thickening in most adults which obscures details of the proximal end. Even the attempt to distinguish obverse from reverse views is often impossible, although it generally appears that $th1^1$ leaves the sicula above the sicular aperture while $th1^2$ extends downwards from the actual aperture. The proximal end is obviously asymmetrical at first. It is possible that the distal apertures of the two stipes do not point in the same plane, at least in the proximal part, and this can lead to apparent differences of width in the two stipes. The level of origin of $th1^1$ on the sicula is sometimes clear and appears to be generally low in the Shelve Llanvirn material, in contrast with the high position recorded by Cooper & Fortey for the true *D. bifidus*. However, the broadening of the sicular area which is produced in this way does not seem to be a useful character in flattened material, since similar broadening certainly occurs as secondary thickening in specimens where the origin of $th1^1$ can be seen to be low.

If the divisions of the old *Didymograptus*, such as *Expansograptus*, are kept as subgenera along with the precisely-defined *Didymograptellus*, it is difficult to provide a suitable nomenclature for all those pendent forms (the majority of the species) whose proximal development is not known, unless *D.* (*Didymograptus*) is regarded as a 'sack' genus. Since there are no pendent didymograptids in the Arenig of Shelve, and therefore presumably no *Didymograptellus*, the pendent forms are all put into *Didymograptus* s.str. for the present. The main nomenclatural problem is then deciding on names for the forms which have hitherto been called *D. bifidus* (Hall). When I first examined the material from the Hope Member many years ago, I identified some of the specimens as *bifidus* and others as *murchisoni*, although according to standard lists the two were not supposed to occur together. With the recent proliferation of names (as noted by Cooper & Fortey 1982: 218) there is no difficulty in finding one to match each specimen, but when populations are considered it is clear that the names do not signify species. Unfortunately the preservation of most of the Shelve specimens is not good enough for consistent measurements to be made and most individual localities have too few specimens for any reliable analysis. The rate of stipe increase, however, using the ratio of width at 10 mm to width at 5 mm, shows a fairly consistent trend in the larger specimens from the Llanvirn which goes some way towards satisfying the subdivision into two zones (Fig. 5).

More recently, Jenkins (1983) has proposed the name *D. pluto* for a wide variety of forms from the Great Paxton borehole, on the assumption that a single variable population is present. He thus includes under one name specimens which Skevington (1973) had referred to *D. acutus* Ekström, *D. artus* Elles & Wood, *D. murchisoni* (Beck), *D. speciosus* Ekström and *D.* cf. *geminus* (Hisinger), and incidentally changes the horizon from Upper to Lower Llanvirn. Jenkins, however, believes that all the pendent didymograptids of the rest of Britain have $th1^1$ dicalycal while *D. pluto* has $th1^2$ dicalycal, and therefore concludes that the Great Paxton graptolites have no connection with those of Wales and the Welsh Borders. Since the material from Shelve of both *D.* '*bifidus*' and *D. murchisoni* can be shown to have $th1^2$ dicalycal in some specimens, there is no need to regard the Great Paxton material as being in a totally different province, as indeed the similarities in the trilobites (which Jenkins ignores) demonstrate, and the relationship of *D. pluto* to the range of forms at Shelve needs to be considered. An exactly

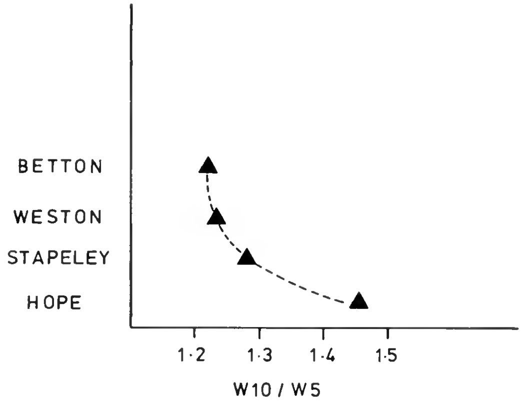


Fig. 5 Mean values of the ratio of stipe width at 10 mm and 5 mm from the sicula for pendent didymograptids of *murchisoni*-type in relation to horizon.

similar range of forms can be found in the Hope Member but neither preservation nor abundance is good enough to allow real statistical comparison. From the little which can be done, it is clear that the average figures agree fairly well with Jenkins' study. If this approach to populations is approved, then the naming of specimens from different localities becomes very difficult as Cooper (1973) demonstrated for *Isograptus*. Individual morphotypes have a long range. If stratigraphical usefulness is required, the population approach gives good results but single specimens cannot be given a precise name. Jenkins provides only two differences between *D. pluto* and *D. murchisoni*, but since some at least of *D. murchisoni* have th1^2 dicalycal, his only remaining difference is that *murchisoni* has a slightly wider thecal spacing on average (14·3 per cm) than *pluto* (17·2 per cm distally): see, however, p. 14. Although the numbers in the Shelve collections are small, a very similar difference in thecal spacing is seen between the specimens from the Hope Member and from the Betton Member, in both the Whittard and the Lapworth collections. One of the main differences given by Nicholson (1870) between '*bifidus*' and *murchisoni* is the greater thecal count in *bifidus*, although the figures he gives are lower than those given by Jenkins.

If this broad concept of a species is accepted, then it is apparent that there are very few species of pendent didymograptids in the Shelve Inlier. The early ones can be called *D. pluto* and the common one in the uppermost Llanvirn clearly matches *D. murchisoni*. There remain a few specimens which cannot easily be fitted into these two. These have comparatively slender stipes which are almost uniform in width and were put by Elles & Wood into their *indentus* Group. Jenkins has illustrated a few specimens of his *D. pluto* which show little if any increase in width of stipes with length and these have clearly a different growth pattern from the rest of his specimens. They are similar to *D. indentus* (Hall) but this Levis species is poorly known and has been largely ignored by American workers. The Russian and Chinese specimens have probably been assigned to it mainly on the thecal count. *D. stabilis* and *D. miserabilis* have the same growth pattern. In contrast *D. artus*, which Elles & Wood put in this group, does not, having the more usual continued increase. There are too few specimens in the Shelve collections to allow any analysis of character range in these forms and so they will be treated as separate species for the present.

Didymograptus murchisoni (Beck 1839)
Pl. 3, figs 8, 9, 11–14

1839 *Graptolithus Murchisonii* Beck *in* Murchison: 694; pl. 26, figs 4, 4a.
1901 *Didymograptus Murchisoni* (Beck); Elles & Wood: 37; pl. 3, figs 1a–k; text-figs 24a–c.
1901 *Didymograptus Murchisoni* var. *geminus* (Hisinger); Elles & Wood: 40; pl. 3, figs 2a–c, ?d–j; text-figs 25a–c, ?d.
1984 *Didymograptus murchisoni* (Beck); Strachan & Khashogji: 223; figs 1–7.

DESCRIPTION. Rhabdosome variable but generally stout, often 2·5 to 3·0 cm long, widening from 0·75 mm at $th1^1$ to 1·4 mm in the first 10 mm and thereafter to 2·0 mm or even 2·5 mm. The stipes diverge initially at about 90° but rapidly curve to become nearly parallel, although some specimens remain divergent. The sicula has a length of 1·5–2·0 mm and the initial bud appears fairly low down. The proximal end is usually secondarily thickened in mature specimens and details of development obscure, but some specimens show clear indication of isograptid development, $th1^2$ being the dicalycal theca. Thecae number 16 per cm proximally and 14–15 per cm distally. The thecae are simple tubes, curved distally so that they are inclined at about 35° to the dorsal wall of the stipe proximally but at 50°–70° distally. Thecal overlap varies from about half at the proximal end to three-quarters distally. A few large specimens show complete overlap at the distal end where the thecae are very curved and open at right angles to the stipe length.

DISCUSSION. An account of the type material of *D. murchisoni* from the Builth–Llandrindod inlier has been prepared separately (Strachan & Khashogji 1984). If the population approach to species (p. 12) is accepted, then the various forms previously listed from the higher beds of the Llanvirn (Strachan 1981) as *D. pandus*, *D. speciosus*, *D. geminus* and *D. acutus* should all be regarded as within the one species for which *D. murchisoni* is the appropriate name. The distinction between this species and *D. pluto* is probably purely statistical but has stratigraphical usefulness, although it may be difficult to determine where to put the arbitrary boundary. Stratigraphically, the faunas of the Weston Member appear to belong with the Betton Member, particularly in the rate of increase of stipe width as measured by the ratio of width at 10 mm to width at 5 mm which is less than 1·25. In the Hope Member this ratio is 1·4.

MATERIAL AND HORIZONS. The species is the commonest in the Weston and Betton Members where, however, it has few associates. Weston: Q.5212, Lyde Stream; Q.5213, Loc. 444. Betton: Q.5209, Loc. 382A; Q.5210, Loc. 307; Q.5211, Loc. 437; Q.5227, Loc. 536; Q.5344, Loc. 232. The last two localities appear to be at the upper limit of the Betton Member and also contain *Gymnograptus*(?) sp.

Didymograptus pluto Jenkins 1983
Fig. 6; Pl. 2, figs 5–7, 11, 13

1983 *Didymograptus pluto* Jenkins: 642, text-figs 2A, B, 3A, C–G, I–K, M–R, T, U, 4A–C (? *non* figs 3B, H, L, S)

DESCRIPTION. Rhabdosome variable in size and shape but generally with straight stipes 2·0–2·5 cm long, diverging ultimately at 15°–35°. The stipes widen fairly rapidly from an initial 0·5–0·6 mm to 1·0 mm at 5 mm from the sicula and 1·6 mm at 10 mm. The maximum width is rarely more than 2·0 mm although one specimen with a stipe length of 3·7 cm has a width of

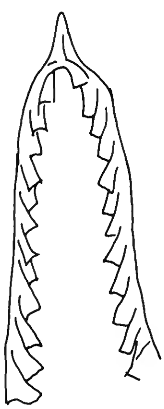


Fig. 6 *Didymograptus pluto* Jenkins. Q.5214, Loc. 169. × 5.

2·4 mm. The thecae number 8–9 in the first 5 mm and about 16 per cm distally. The sicula is 1·2–1·6 mm long and the proximal end of the rhabdosome is frequently thickened so that the details of development cannot be seen. Some specimens, however, show that $th1^2$ is dicalycal and the development is early isograptid.

Discussion. Jenkins (1983) has described the species on the basis of population studies and although it is very varied morphologically there appears to be good evidence for it being a single species. It probably represents most of what British authors have previously called *D. bifidus*, from which it is distinguished by the much longer sicula and low position of the initial bud. It appears to be only statistically different from *D. murchisoni*, the main difference being in the thecal count, but there is also a difference in the rate of widening of the stipes, *D. pluto* widening initially much more rapidly than *D. murchisoni*. *D. pluto* includes forms which have previously been referred to *D. murchisoni* and its allies (*geminus*, *speciosus*, etc.), and my preliminary lists from Shelve included these forms from the Hope Member. I am happy to include them now under a single name as stratigraphically and biologically this makes sense. Cooper & Fortey (1982: 224) have suggested that *D. spinulosus* Perner 1895 may be the senior name available for British *D.* '*bifidus*'. This species however is a member of the *indentus* Group of Elles & Wood (see p. 12), having a basically uniform width of the more or less parallel stipes.

Material and horizons. Hope Member: Q.5214, Q.5220, Loc. 169; Q.5215, Loc. 54; Q.5216, Loc. 222A; Q.5218, Loc. 834; Q.5219, Loc. 204; Q.5221, Loc. 959; Q.5224, Loc. 635. Stapeley Member: Q.5217, Q.5222, Q.5223, all Loc. 133.

D. pluto is the common form certainly in the Hope Member and probably also in the succeeding Stapeley Member, but there are too few specimens in the latter for an adequate comparison. In the Hope Member it is associated with extensiform didymograptids as well as rare phyllograptids. In the Stapeley Member, the pendent didymograptids are found with rare *Glossograptus* and *Acrograptus*.

Didymograptus aff. ***miserabilis*** Bulman 1931
Fig. 7

aff. 1931 *Didymograptus miserabilis* Bulman: 40; pl. 2, fig. 12.

Description. Stipes up to 1 cm long and 0·8 mm wide, parallel for most of their length. Thecae number 15 to 16 per cm. The sicula is slender and about 1 mm long.

Discussion. Only two specimens have been found of this small, slender species and neither is well preserved. However, it is clear that they are not just young specimens of the larger forms, nor can they be fitted into the range of any reasonable population spectrum of such forms. The sicula is shorter than reported by Bulman but it is clearly broken in one specimen.

Material and horizons. One specimen, Q.5225, occurs in the Stapeley Member, Loc. 463, and one in the Betton Member, Q.5226, Loc. 536, where it is associated with *D. murchisoni*, a similar horizon to the Peruvian occurrence.

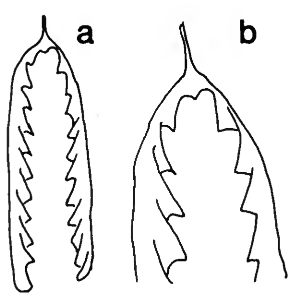


Fig. 7 *Didymograptus* aff. *miserabilis* Bulman. Q.5225, Loc. 463. a, ×5; b, proximal end ×10.

Didymograptus cf. **_stabilis_** Elles & Wood 1901
Fig. 8; Pl. 2, fig. 8

cf. 1901 *Didymograptus stabilis* Elles & Wood: 49; pl. 4, fig. 2; text-figs 31a, b.

DESCRIPTION. Stipes up to 3 cm long but usually much shorter, diverging initially at about 90° but rapidly becoming subparallel; widening from 0·5 mm to 1·3 mm in the first 10 mm and then uniform, although long specimens may reach 1·6 mm width. Thecae number 18 to 20 per cm; sicula 1·5–1·8 mm long, slender with initial bud appearing fairly low, $th1^2$ dicalycal, proximal end thickened in old specimens.

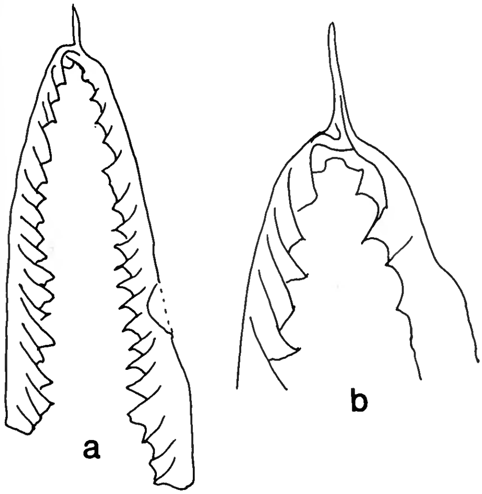


Fig. 8 *Didymograptus* cf. *stabilis* Elles & Wood. Q.5228, Hope Member, exact locality unknown. a, ×5; b, proximal end ×10.

DISCUSSION. Although the thecal count of the Shelve specimens is much higher than that given by Elles & Wood, they fit this species in general form, i.e. parallel stipes, medium size and long sicula. As I believe that *D. artus* has the different growth form of continual increase in width with length (whatever may be the realities of its proximal development), the high thecal count must be taken as parallelism.

MATERIAL AND HORIZONS. Hope Member: Q.5229, Loc. 635; Q.5230, Loc. 140. Stapeley Member: Q.5232, Loc. 133. Betton Member: Q.5231, Loc. 307. The form is fairly common in the Hope and Stapeley Members but appears to be rare in the Betton Member.

Genus **_EXPANSOGRAPTUS_** Bouček & Přibyl, 1951

TYPE SPECIES. *Graptolithus extensus* Hall 1858.

Cooper & Fortey (1982) have discussed the problems of taxonomy of extensiform didymograptids but retain both *Expansograptus* and *Corymbograptus* as subgenera of *Didymograptus*. As noted above, this leaves the nomenclature of pendent forms whose development is unknown in a very unsatisfactory state, as *Didymograptus* s.str. becomes a 'sack' genus, a contradiction in terms. I prefer to keep *Expansograptus* and *Corymbograptus*, unsatisfactory groupings as they are, at generic level from the practical point of view along with *Acrograptus* (which Cooper & Fortey accept only because they put it in a separate subfamily). There seems little point at the moment in stressing the development of the proximal end in the nomenclature when so little is known and some at least of the statements which have been made about development in particular cases are wrong. These generic names have been around for quite a long time now and need refining (like many others), but this cannot be done until we have a better understanding of the nature of the actual species involved. There are virtually no population studies available but a multitude of names, many of which are probably synonyms, and

no modern stratigraphical studies of the classic type areas. Until the range of species in populations and the stratigraphical range of such forms is adequately documented, discussion on phylogenetic units is meaningless. For example, if *D.* (*E.*) *extensus* (Hall) (Cooper & Fortey 1982: 231) is restricted to forms in which the branches diverge immediately from the sicula and consequently British '*extensus*' can no longer be incorporated in it, can *D. nitidus* (Hall) show enough variation in proximal end shape to accommodate the British '*extensus*'? Probably it can (and I have done so here) but Elles & Wood noted that *nitidus* in Britain seemed more variable than the Canadian types. If *extensus* was absent from the boreal realm (Cooper & Fortey 1982: 234), which implies a particular Arenig palaeogeography, are the boreal forms more variable than the tropical ones and what are the implications of this for comparative taxonomy?

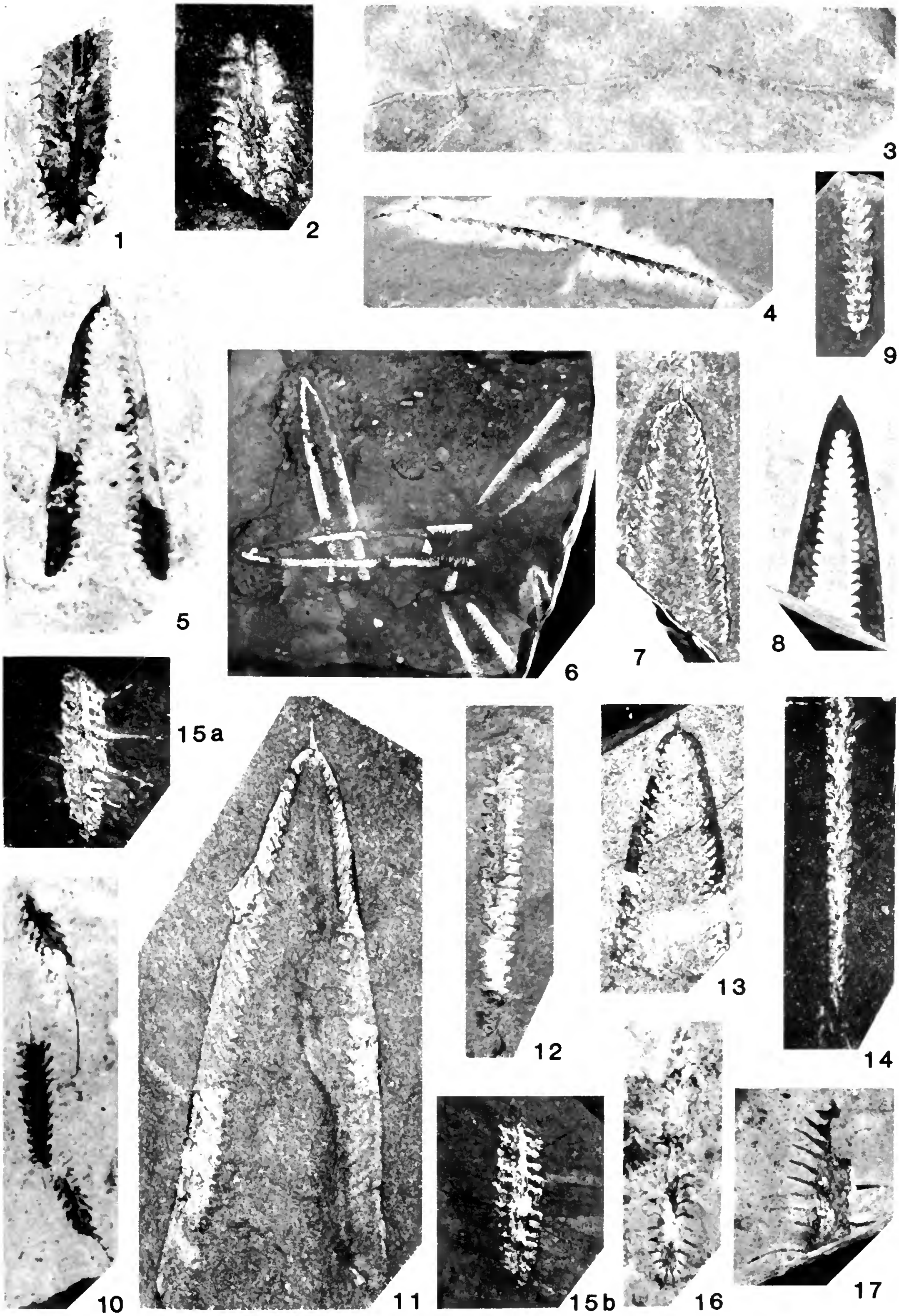
Expansograptus cf. ***euodus*** (Lapworth 1875)

cf. 1875 *Didymograptus euodus* Lapworth: 645; pl. 35, figs 1a–c.
cf. 1901 *Didymograptus euodus* Lapworth; Elles & Wood: 21; pl. 1, figs 10a, b; text-fig. 12.

A single long dichograptid stipe without proximal end appears to belong to this species. It is 15 cm long and has a uniform width of about 2 mm. The thecae are simple, slightly curved tubes, overlapping about half of their length and there are 8 per cm. The angle of inclination appears to be higher than given by Lapworth (30°–40°) but the curvature of the thecae makes exact measurements difficult. In the absence of a proximal end, only general comparison can be made and of the species recorded from Britain at about this horizon *E. euodus* appears to be the best fit. The specimen (Q.5233) is associated with numerous pendent didymograptids characteristic of the Hope Member, at Loc. 169.

PLATE 2 Figs 1–12, 14, 15 from the Hope Member; Figs 13, 16, 17 from the Stapeley Member.

Fig. 1 *Pseudophyllograptus* cf. *angustifolius* (Hall), p. 10. Q.5207a, Loc. 635. ×3. See also Text-fig. 3, p. 10.
Fig. 2 *Pseudophyllograptus*(?) cf. *glossograptoides* (Ekström), p. 10. Q.5208a, Loc. 922. ×3. See also Text-fig. 4, p. 10.
Figs 3, 4 *Acrograptus acutidens* (Elles & Wood), p. 22. Fig. 3, BU.2077 (Lapworth Collection), Ritton Castle, Shelve. ×2. Fig. 4, Q.5249, Loc. 701. ×3. See also Text-fig. 15, p. 22.
Figs 5–7 *Didymograptus pluto* Jenkins, p. 13. Fig. 5, Q.5215, Loc. 54. ×3. Fig. 6, Q.5216, Loc. 222A. ×1. Fig. 7, BU.2078 (Lapworth Collection), Snailbeach Stream (Hogstow Brook). ×3.
Fig. 8 *Didymograptus* cf. *stabilis* Elles & Wood, p. 15. Q.5229, Loc. 635. ×3.
Fig. 9 *Amplexograptus* cf. *confertus* (Lapworth), p. 36. Q.5303, Loc. 959. ×3.
Fig. 10 *Glyptograptus dentatus* (Brongniart), p. 37. Q.5308, Loc. 701. ×3. See also Pl. 1.
Fig. 11 *Didymograptus pluto* Jenkins, p. 13. BU.2079 (Lapworth Collection), Snailbeach Stream (Hogstow Brook). ×3.
Fig. 12 *Glyptograptus* sp., p. 39. Q.5310, Loc. 959. ×3. See also Text-fig. 33, p. 39.
Fig. 13 *Didymograptus pluto* Jenkins, p. 13. Q.5217, Loc. 133. ×3.
Fig. 14 *Climacograptus* cf. *angustatus* Ekström, p. 41. Q.5324 (Illing collection), Hope Member, exact locality unknown. ×3.
Fig. 15a, b *Glossograptus* cf. *armatus* (Nicholson), p. 24. Q.5256 (Illing Collection), Hope Member, exact locality unknown. Two views to show different detail. ×3. See also Text-fig. 20, p. 24.
Fig. 16 *Glossograptus fimbriatus* (Hopkinson), p. 24. Q.5255, Loc. 133. ×3. See also Text-fig. 19, p. 24.
Fig. 17 *Glossograptus* cf. *acanthus* Elles & Wood, p. 23. Q.5254, Loc. 132. ×3. See also Text-fig. 18, p. 24.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Expansograptus cf. *hirundo* (Salter 1863)
Pl. 1, fig. 9

cf. 1863 *Didymograpsus hirundo* Salter: 137, fig. 13f.
cf. 1901 *Didymograptus hirundo* Salter; Elles & Wood: 15; pl. 1, figs 5a–c; text-figs 9a–c.

DESCRIPTION. Stipes up to 6 cm long, widening from 1·6 mm at $th1^1$ to 2·2 mm at th5 and probably continually afterwards but more slowly, the longest stipes having widths of 2·5–2·8 mm. Thecae 12 to 10 per cm, strongly curved at the proximal end and inclined at 60°–80°, overlapping three-quarters or more.

DISCUSSION AND OCCURRENCE. A single specimen (Q.5234) shows the compact proximal end characteristic of *E. hirundo* and a number of long stipe fragments have thecae with a fairly high inclination which match those figured by Elles & Wood. They occur in the uppermost part of the Mytton Member (Rhodes locality, Tankerville Flags).

Expansograptus cf. *nitidus* (Hall 1858)
Pl. 1, figs 2–5

cf. 1858 *Graptolithus nitidus* Hall: 129.
cf. 1901 *Didymograptus nitidus* (Hall); Elles & Wood: 10; pl. 1, figs 2a–c; text-figs 5a–d.
cf. 1982 *Didymograptus* (*Expansograptus*) *nitidus* (Hall); Cooper & Fortey: fig. 40f, g.

DESCRIPTION. Stipes up to 2 cm long, diverging at varying angles from the sicula but rapidly becoming horizontal, widening fairly rapidly from 0·8–1·0 mm at th1 to a maximum of 1·6 mm. Thecae 12 to 10 per cm. Sicula 1·4–1·6 mm long, $th1^1$ arising near the apex, development of isograptid type.

DISCUSSION. Following the redescription of *E. extensus* by Cooper & Fortey (1982), stressing the initial horizontal growth of the stipes in that species, forms which had previously been identified as *D. extensus* have been grouped with those of *E. nitidus* from Shelve. The distinction made earlier (Strachan 1981) was based on the amount of proximal curvature, the more curved forms being put in *nitidus* (as *Corymbograptus*), the less curved forms as *extensus* relying on Elles & Wood's description. Most of the specimens are deformed to some extent so that detailed comparative measurements are impossible but the specimens all appear to be wider proximally than in Canadian material. However, the sicular details are similar and also agree with those of *E. extensus*, so they are placed in *Expansograptus*.

MATERIAL AND HORIZON. The species occurs in the Mytton Member and is fairly common at Shelve Church (Loc. 720: Q.5235–7). It is also found at Bergam Quarry (Loc. 783: Q.5238).

Expansograptus cf. *praenuntius* (Törnquist 1901)
Fig. 9

cf. 1901 *Didymograptus praenuntius* Törnquist: 17; pl. 2, figs 7–12.
cf. 1982 *Didymograptus* (*Expansograptus*) *praenuntius* Törnquist; Cooper & Fortey: 235; fig. 43a, b; pl. 4, fig. 12.

DESCRIPTION. Stipes 10 mm long, widening rapidly from 1·2 mm at th1 to 1·7 mm at th4, then uniform, extending horizontally from the sicula. Thecae 10 per cm. Sicula 2·2 mm long.

Fig. 9 *Expansograptus* cf. *praenuntius* (Törnquist). Q.5239, Loc. 783, Bergam Quarry. a, $\times 2\frac{1}{2}$; b, proximal end, $\times 5$.

Discussion and occurrence. A single specimen (Q.5239) in the collection was identified as this species by O. M. B. Bulman and agrees fairly well with the most recent account by Cooper & Fortey. The specimen is from Bergam Quarry (Loc. 783) in the highest part of the Mytton Member and this occurrence strongly supports the view that the Mytton Member is largely pre-*hirundo* Zone. There are, however, broad stipes associated with it which Bulman identified as *D. hirundo* and a single proximal end, possibly from the same locality, has something of the compact structure seen in *hirundo*. Since there are only some 20 specimens from the quarry, most of which are single stipe fragments, the real nature of the population is uncertain.

Expansograptus cf. ***simulans*** (Elles & Wood 1901)
Pl. 1, fig. 7

cf. 1901 *Didymograptus simulans* Elles & Wood: 30; pl. 2, figs 6a, b; text-figs 19a–c.

Description. Stipes 2·5 cm long, diverging from the sicula at 135° but soon becoming horizontal, width 0·4 mm initially, widening slowly to 0·8 mm. Thecae 14 to 12 per cm, inclined at 25°–30°, overlapping less than half in the proximal thecae but half to two-thirds distally. Sicula short, 0·8 mm long.

Discussion and occurrence. Two poorly preserved specimens (Q.5242, Loc. 905 and Q.5243, Loc. 853A) from the Mytton Member are clearly allied to this species. In appearance it is somewhat like a rather slender *E. nitidus*, having a similar proximal curvature. It does not seem to have been recognized elsewhere. The specimen figured by Mu *et al.* (1979) as *D.* cf. *simulans* is more robust at the proximal end, as was noted by the Chinese authors.

Expansograptus cf. ***sparsus*** (Hopkinson 1875)

cf. 1875 *Didymograptus sparsus* Hopkinson: 643; pl. 33, figs 2a–d.
cf. 1901 *Didymograptus sparsus* Hopkinson; Elles & Wood: 17; pl. 1, figs 6a, b; text-fig. 10.

Another long dichograptid stipe occurs as a single specimen, Q.5244, from the Mytton Member at Shelve Church, Loc. 720. It is also about 15 cm long and has a uniform width of about 2 mm. It is poorly preserved and is noteworthy only for its length. The thecae number about 7 per cm and are simple tubes, overlapping about half of their length and inclined at about 45°. The stipe is too narrow for one of the large tetragraptids which might be expected to occur at this horizon and although there is some distortion of the specimen, the thecae are markedly fewer than in some other stipes of similar width but much shorter length which could be attributed to forms like *hirundo*.

Expansograptus cf. ***suecicus*** (Tullberg 1880)
Fig. 10

cf. 1880 *Didymograptus suecicus* Tullberg: 43; pl. 2, figs 15, 16.
cf. 1974 *Expansograptus suecicus* (Tullberg); Tzaj: 79; pl. 7, figs 6, 7; text-fig. 20.

Description. Stipe 10 mm long, widening from 1·0 mm to 1·8 mm, diverging at 120° from the sicula but quickly becoming horizontal. Thecae simple tubes, 13 to 12 per cm, inclined at about 50°, overlapping a half to two-thirds. Sicula about 1·6 mm long.

Discussion and occurrence. A single specimen from Bergam Quarry (Q.5245, Loc. 783) in the uppermost Mytton Member has some of the characters of this species but has a higher thecal count. It is wider than the associated *E.* cf. *praenuntius* but a large collection might well show intermediate forms. There is nothing precisely to match it amongst Monsen's (1937) many species. *D. enshiensis* Ni (*in* Mu *et al.* 1979) is similar but probably more curved. The precise attitude of the stipes in this specimen is uncertain since one is broken off at the sicula.

Fig. 10 *Expansograptus* cf. *suecicus* (Tullberg). Q.5245, Loc. 783. × 5.

Genus *CORYMBOGRAPTUS* Obut & Sobolevskaya, 1964

TYPE SPECIES. *Didymograpsus V-fractus* Salter 1863.

Although not specifically mentioned in the original description, this genus appears to be based essentially on Elles & Wood's deflexed series, in which the proximal end forms part of a V-shape with the stipes at first dorsally convex and later concavely curved. Tzaj (1974) lists twelve species in the genus but most of these approach the extensiform type rather than the *v-fractus* type. Cooper & Fortey (1982: 239) express reservations on their use of *Corymbograptus* as a subgenus but their *D. v-fractus* from Spitsbergen is nothing like Salter's species and their *D.* cf. *deflexus*, although clearly a *Corymbograptus*, is not very close to Elles & Wood's form. This, and their correlation of the Chinese horizons which differs from that of Mu *et al.* (1979), may have unduly influenced them. A characteristic feature of *Corymbograptus* is that the initial growth of the stipes is dorsally convex, like those of pendent didymograptids, and not concave like *E. nitidus*. All the forms with this curvature figured by Mu *et al.* (1979) are from their N3 horizon, which they equate with the lowest part of the Arenig sequence in Britain and therefore contemporary with the British forms.

Corymbograptus deflexus (Elles & Wood 1901)
Fig. 11; Pl. 1, fig. 1

1901 *Didymograptus deflexus* Elles & Wood: 35; pl. 2, figs 12a–c; text-figs 23a, b.
1933 *Didymograptus deflexus* Elles & Wood; Elles: text-fig. 13.
non 1934 *Didymograptus deflexus* Elles & Wood; Hsü: 36; pl. 2, figs 7a–c.
non 1937 *Didymograptus* cf. *deflexus* Elles & Wood; Monsen: 146; pl. 3, figs 38, 41; pl. 10, fig. 12.
non 1974 *Corymbograptus deflexus* (Elles & Wood); Tzaj; 82; pl. 8, figs 1–4.

DESCRIPTION. The sicula is 2 mm long and has a short nema. The first theca arises halfway down the sicula and gives rise to the crossing canal of the second theca almost immediately. The rest of the development cannot be seen in this specimen since it is partially broken away. $Th1^1$ diverges from the sicula above the sicular aperture but $th1^2$ grows down past the aperture. The dorsal wall of the stipe is at first convex and the stipes diverge at about 70° in the V-shape. After five or six thecae, the stipes curve again to become horizontal. The stipes reach a width of 1·5 mm and the thecae number 12 per cm.

DISCUSSION. Elles (1898) first described this form as a young stage of *C. v-fractus* but in the Monograph (Elles & Wood 1901) distinguished it as a separate species. It has the curvature of the stipes characteristic of the genus but is in all respects a smaller form than the type species. It is rare at Shelve, being represented by only one specimen in the Whittard collection, which, however, matches the holotype very closely in size and curvature of the stipes.

The species has been recorded from China, Kazakhstan and Australia but the specimens figured from the two former areas do not show the fairly sharp demarcation between the proximal V-shape and the distal extension of the stipes. Although Thomas (1960) lists the species, it does not seem to have been described from Australia and Cooper (1979) notes that one of Monsen's '*D.* cf. *deflexus*' from Norway is close to the Australasian *D. v-deflexus* Harris.

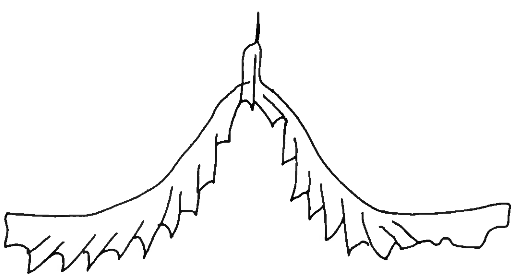


Fig. 11 *Corymbograptus deflexus* (Elles & Wood). Q.5246, Loc. 720[1]. Drawing of Pl. 1, fig. 1, ×5.

The Spitsbergen specimens figured by Cooper & Fortey (1982) have a much longer proximal section before the stipes turn outward.

MATERIAL AND HORIZON. The specimen, Q.5246, is from the Mytton Member at Shelve Church, Loc. 720.

Corymbograptus cf. ***inflexus*** (Chen & Xia 1979)
Fig. 12; Pl. 1, fig. 6

cf. 1979 *Didymograptus inflexus* Chen & Xia, *in* Mu *et al.*: 84; pl. 29, figs 8–11.

DESCRIPTION. Stipes up to 15 mm long, widening from 0·8 mm at the proximal end to 1·2 mm at 5 mm from the sicula, and remaining at that width. Thecae 7 to 6 in 5 mm, generally curved. Sicula 1·4 mm long, curved. The stipes diverge at about 125° from the sicula and are curved with convex dorsal margin for about 5 mm to make an angle of about 100° before flexing again to become sub-horizontal.

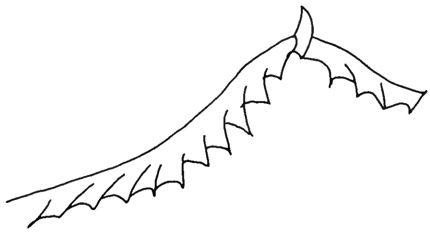


Fig. 12 *Corymbograptus* cf. *inflexus* (Chen & Xia). BU.2075, Shelve Church. Drawing of Pl. 1, fig. 6, × 5.

DISCUSSION AND OCCURRENCE. This single specimen (BU.2075) from the Shelve Church Beds (Loc. 720) is in general form close to one of the illustrations in Mu *et al.* (1979) of *D. inflexus* and the measurements match that species best of the 25 forms described in the volume. Other forms such as *D. aequus* Ni are similar but have wider stipes proximally or fewer thecae per cm. This species has the initial dorsal curvature of the stipe characteristic of *Corymbograptus* although many of the other 'deflexed' forms do not. The sicula appears to be distinctly curved towards the second stipe, a feature also noted by the Chinese workers for *C. deflexus* although not particularly noticable in Elles & Wood's (1901) figures. All the Chinese deflexed forms are from the *deflexus* Zone, well below their *hirundo* horizon, and this would confirm the suggestion above (p. 4) that the Shelve Church Beds of the Mytton Member are not as late as the *hirundo* Zone, although some workers have claimed this.

Subfamily **ISOGRAPTINAE** Harris, 1933

Genus ***ISOGRAPTUS*** Moberg, 1892

TYPE SPECIES. *Didymograptus gibberulus* Nicholson 1875.

Isograptus sp.
Fig. 13; Pl. 1, fig. 8

DESCRIPTION. A single specimen in the Whittard Collection (Q.5247) is a broken but well-preserved isograptid which cannot be matched with any described form. The sicula is 3 mm long with a further 2·5 mm of nema. The first theca is almost as long as the sicula and diverges from it only in the last part, leaving a deep notch between the two which is emphasized by the long stout processes on both (and on all the subsequent thecae). The width of the stipes at the flexure is 2·0 mm but they seem to narrow distally, a real narrowing since the apertural processes are present. The dorsal curvature of the stipes is asymmetrical in relation to the sicula but is comparatively gentle, suggesting an angle of 120° (240° between the ventral margins), a much greater angle of divergence than in most species of *Isograptus*. The longer of the two stipes is only 5 mm but there are 9 thecae, a much closer arrangement than in any described species.

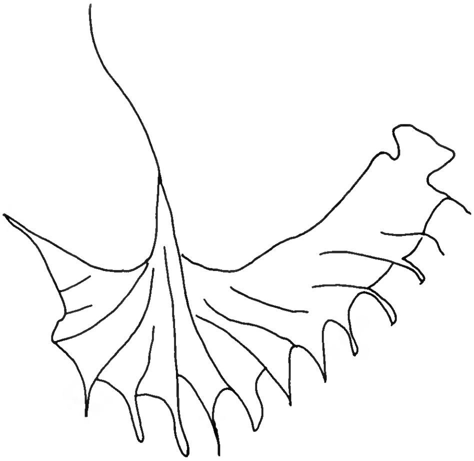


Fig. 13 *Isograptus* sp. Q.5247, Loc. 791. Drawing of Pl. 1, fig. 8, × 10.

DISCUSSION AND OCCURRENCE. Jenkins (1982) has attempted a redefinition of *Isograptus* but unfortunately he states that Moberg's original description was based on material from Öland when in fact all the figures are material from Killeröd which Jenkins claims is a different form. None of the forms which Jenkins figures from Britain bear any close resemblance to this single specimen from Shelve which unfortunately was found by itself at Loc. 791, mapped by Whittard as Mytton Member. There is no counterpart so details of proximal development are incomplete.

Subfamily **SIGMAGRAPTINAE** Cooper & Fortey, 1982

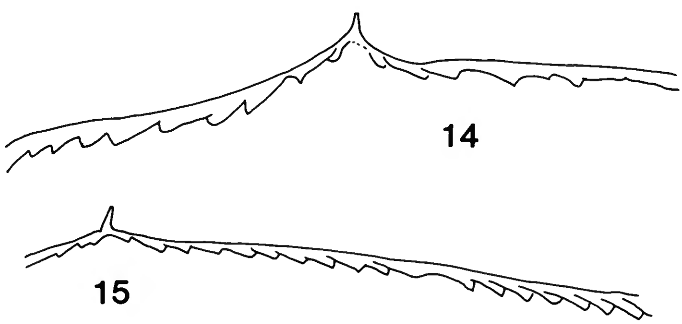
Genus ***ACROGRAPTUS*** Tzaj, 1969

TYPE SPECIES. *Didymograptus affinis* Nicholson 1869.

Acrograptus acutidens (Elles & Wood 1901)
Figs 14, 15; Pl. 2, figs 3, 4

1901 *Didymograptus acutidens* Lapworth MS; Elles & Wood: 25; pl. 2, figs 3a–d; text-figs 15a–c.

DESCRIPTION. Stipes straight, several cm long with a maximum width of 1 mm. Sicula prominent, about 1 mm long, the first thecae diverging from its aperture at about 150°; the width at $th1^1$ is 0·3 mm. Thecae 13 per cm, inclined at 20° to the stipe length and with considerable overlap distally.



Figs 14, 15 *Acrograptus acutidens* (Elles & Wood). Fig. 14, Q.5248, Loc. 54; Fig. 15, Q.5249, Loc. 701, drawing of Pl. 2, fig. 4. Both × 5.

DISCUSSION. Tzaj (1969) included this slender species in his original account of *Acrograptus* although the stipes are nearly horizontal. The species is one of Lapworth's MS forms from Shelve and was first described by Elles & Wood. The specimens are not well enough preserved to show details of development as there seems to be some thickening around the proximal end. One specimen (Fig. 14) shows similar slender stipes with greater proximal curvature approaching that seen in *E. nitidus*.

MATERIAL AND HORIZON. The species occurs in the Hope Member. Q.5248, Loc. 54; Q.5249, Loc. 701; Q.5250, Q.5251, Loc. 834N.

Acrograptus gracilis (Törnquist 1890)
Figs 16, 17

1890 *Didymograptus gracilis* Törnquist: 17; pl. 1, figs 9–12.
1901 *Didymograptus gracilis* Törnquist; Elles & Wood: 24; pl. 2, fig. 2; text-figs 14a, b.
1982 *Acrograptus gracilis* (Törnquist); Cooper & Fortey: 272; figs 66c–g.

DESCRIPTION. Stipes up to 1 cm long, very slender, widening from 0·3 mm to 0·5 mm. Sicula long and slender, initial bud appearing in upper half. First two thecae turning laterally at the sicular aperture and soon extending horizontally. Thecae long and slender, about 11 per cm, overlapping about one third, with simple apertures.

DISCUSSION. This very slender species was included in the original account of *Acrograptus* (Tzaj 1969), although the stipes extend horizontally. As with *A. acutidens*, the proximal end is clearly different from the *Expansograptus* type and these generally slender forms may well be phylogenetically related with the stipe attitude variable.

MATERIAL AND HORIZON. The species is rare in the Hope Member but the slender stipes are easily overlooked. Q.5252, Loc. 54; Q.5253, Loc. 58.

Figs 16, 17 *Acrograptus gracilis* (Törnquist). Fig. 16, impression of reverse view, Q.5252a; Fig. 17, counterpart showing impression of obverse view, Q.5252b. Both Loc. 54, × 5.

Family **GLOSSOGRAPTIDAE** Lapworth, 1873

Genus ***GLOSSOGRAPTUS*** Emmons, 1855

TYPE SPECIES. *Glossograptus ciliatus* Emmons 1855.

Surprisingly, only three specimens of this genus have been found in the Whittard Collection. Whittard recorded *G.* cf. *acanthus* in his 1931 paper but the genus does not seem to have been recorded elsewhere from Shelve. *G. hincksi* has been used as a zonal index in Scandinavia and is quite common in the Ordovician of the south of Scotland and in Ireland, so its absence from the Welsh Borders is unexpected. Some 30 species and subspecies have been described to date, but the known complexity of the spines and other processes allows differing views of the same specimen to appear quite different, and it is probable that many of the described forms are synonyms.

Glossograptus cf. ***acanthus*** Elles & Wood 1908
Fig. 18; Pl. 2, fig. 17

cf. 1908 *Glossograptus acanthus* Elles & Wood: 314; pl. 33, figs 4a–c; text-figs 208a, b.

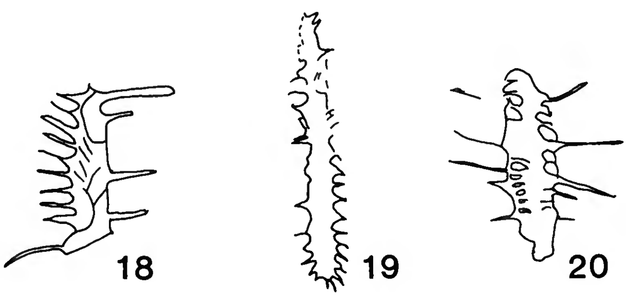
A single distal fragment appears to belong to this species (Q.5254). The specimen is 8 mm long and the width of 2 mm, excluding the spines, is rather narrow for *G. acanthus* but the stout

thecal spines suggest that species. The more distantly placed septal spines project at right angles to the rhabdosome and are also long (up to 4 mm) and stout. This view, showing thecal spines on one side and septal spines on the other, is one which is not illustrated by Elles & Wood but shown by Hadding (1915: pl. 5, fig. 6) for *G. hincksi* and was the basis of his reconstruction of the rhabdosome as a monopleural series. Other authors, however, have not figured the septal spines in this species. *G. minor* Mu, Geh & Yin 1962 is known only as proximal ends up to 6 mm long and there is no information on septal spines, but its general size and thecal type are similar to the specimen here. In *G. holmi*, Bulman (1931: 69) specifically notes that the biprofile width is 3–4 mm but in scalariform view the width is only 2·5 mm. The relative narrowness of this specimen compared with Elles & Wood's range for the species may result from the different preservational view. The thecal count, 12 per cm, is slightly higher than the figure given by Elles & Wood (10 per cm) but their plate shows specimens with more than 10. The horizon, Stapeley Member (Loc. 132), is right for this species.

Glossograptus fimbriatus (Hopkinson 1872)
Fig. 19; Pl. 2, fig. 16

1872 *Diplograptus fimbriatus* Hopkinson: 506; pl. 12, fig. 8.

A second single specimen (Q.5255) from the Stapeley Member (Loc. 133) is a more or less complete rhabdosome about 14 mm long, in biprofile view. The thecae number 14 per cm and are provided with short but stout recurved processes up to 1 mm long. The width, excluding the spines, is 1·6 mm. The distal part is poorly preserved and details of the proximal end are difficult to interpret. There seems to be a long central sicula but the rest of the proximal thecae can only be traced from the apertural spines which point downwards. In general size and form, it matches the specimen figured by Elles (1898) from the Skiddaw Slates, an earlier horizon than that from which Hopkinson originally described the species. Mu & Lee (1958) figured the species with similar dimensions from the Ningkuo Shale (*Expansograptus hirundo* Zone), so the species appears to have a long range.



Figs 18–20 *Glossograptus* spp. Fig. 18, *G.* cf. *acanthus* Elles & Wood. Q.5254, Loc. 132 (Pl. 2, fig. 17). Fig. 19, *G. fimbriatus* (Hopkinson). Q.5255, Loc. 133 (Pl. 2, fig. 16). Fig. 20. *G.* cf. *armatus* (Nicholson). Q.5256, Hope Member, exact locality unknown (Pl. 2, fig. 15). All $\times 2\frac{1}{2}$.

Glossograptus cf. *armatus* (Nicholson 1869)
Fig. 20; Pl. 2, fig. 15a, b

cf. 1869 *Diplograpsus armatus* Nicholson: 234; pl. 11, fig. 8.
cf. 1908 *Glossograptus armatus* (Nicholson) Elles & Wood: 312; pl. 33, figs 5a–e, text-fig. 207.

The third glossograptid from Shelve is from the lower horizon of the Hope Member (Q.5256, Illing Collection) and is a slightly sheared specimen showing very long, stout septal spines. Traces of the thecae can be seen, some of which bear shorter spines. The proximal end is damaged. The rhabdosome is 10 mm long and has a width of 2·4 mm exclusive of the long spines, which can reach a length of 3·5 mm. Nicholson's original description was based on poorly preserved material but Elles' (1898) account seems to be too restrictive as to size. The

later description in the Monograph (Elles & Wood 1908) is largely based on younger Scottish specimens and lays particular emphasis on the long proximal spines. These are well shown on Chinese specimens assigned to this species (Mu *et al.* 1962), where they are described as up to 7 mm long. The thecal count is given as 6 to 7 in 5 mm, which agrees with my estimate of the Shelve specimen and is higher than the figure given by Elles & Wood (9 per cm).

Genus *CRYPTOGRAPTUS* Lapworth, 1880

TYPE SPECIES. *Diplograpsus tricornis* Carruthers 1858.

Recent work on the proximal end of *C. tricornis* shows that *Cryptograptus* has the same general development as *Glossograptus* and so the two genera can be kept in the same family (Strachan 1985).

Cryptograptus tricornis (Carruthers 1858)
Pl. 6, fig. 7

1858 *Diplograpsus tricornis* Carruthers: 468, text-fig. 2.
1969 *Cryptograptus tricornis* (Carruthers); Strachan: 194; pl. 4, figs 4–6; text-fig. 3c (with synonymy).

DISCUSSION. A number of specimens from the Aldress Member show the characteristic features of this species. The rhabdosome is widest at the proximal end (about 1·2 mm) and generally tapers distally. The thecae number 12 per cm and some of the specimens show the basal spines clearly. A few slabs have the surface crowded with specimens but the species is more usually represented by single specimens at each locality.

MATERIAL. Q.5257, Loc. 343; Q.5258, Loc. 395; Q.5259, Loc. 355.

Cryptograptus schaeferi Lapworth 1880
Fig. 21; Pl. 3, fig. 6

1880 *Cryptograptus tricornis* var. *Schaeferi* Lapworth: pl. 5, figs 5a, b.
1908 *Cryptograptus tricornis* var. *Schäferi* Lapworth; Elles & Wood: 299; pl. 32, figs 13a–c; text-figs 201a, b.
cf. 1970 *Cryptograptus tricornis schaeferi* Lapworth; Skevington: 418; text-figs 6a–h, 7a–d.

A few specimens of *Cryptograptus* occur in the Meadowtown Member: Q.5260, Loc. 329; Q.5261, Loc. 503. They are not well preserved but none show the characteristic basal spines of *C. tricornis*; instead the few proximal ends in profile view show rather broad processes from the basal thecae. The rhabdosome has a width of about 1·5 mm and the thecae number about 15 per cm proximally, agreeing with Skevington's (1970) account of this species. Some of Skevington's specimens show long basal spines but none of Lapworth's original material from Builth shows this view. It is therefore possible that the material from the Lake District, which is from an earlier horizon in any case, is distinct from the typical *C. schaeferi*. The stratigraphically early records of '*C. tricornis*' are certainly all suspect but they may not all be *C. schaeferi* as Skevington has suggested. It is noteworthy that the genus does not seem to occur in the Shelve district before the Meadowtown Member which, on the basis of its general fauna, cannot be

Fig. 21 *Cryptograptus schaeferi* Lapworth. Q.5260, Loc. 329. Small proximal end, × 5.

older than Llandeilo. Finney (1978), in a discussion of the affinities of *Cryptograptus*, has put *C. schaeferi* as a junior synonym of *C. marcidus* (Hall) but has not designated type material for *marcidus*. Hall's original drawings (1859) include forms with typical *tricornis* basal spines which have led most workers since Carruthers (1858) to include *marcidus* as a junior synonym of *tricornis*.

Family **CORYNOIDIDAE** Bulman, 1945

Genus ***CORYNOIDES*** Nicholson, 1867

TYPE SPECIES. *Corynoides calicularis* Nicholson 1867.

Corynoides cf. ***curtus*** Lapworth 1876

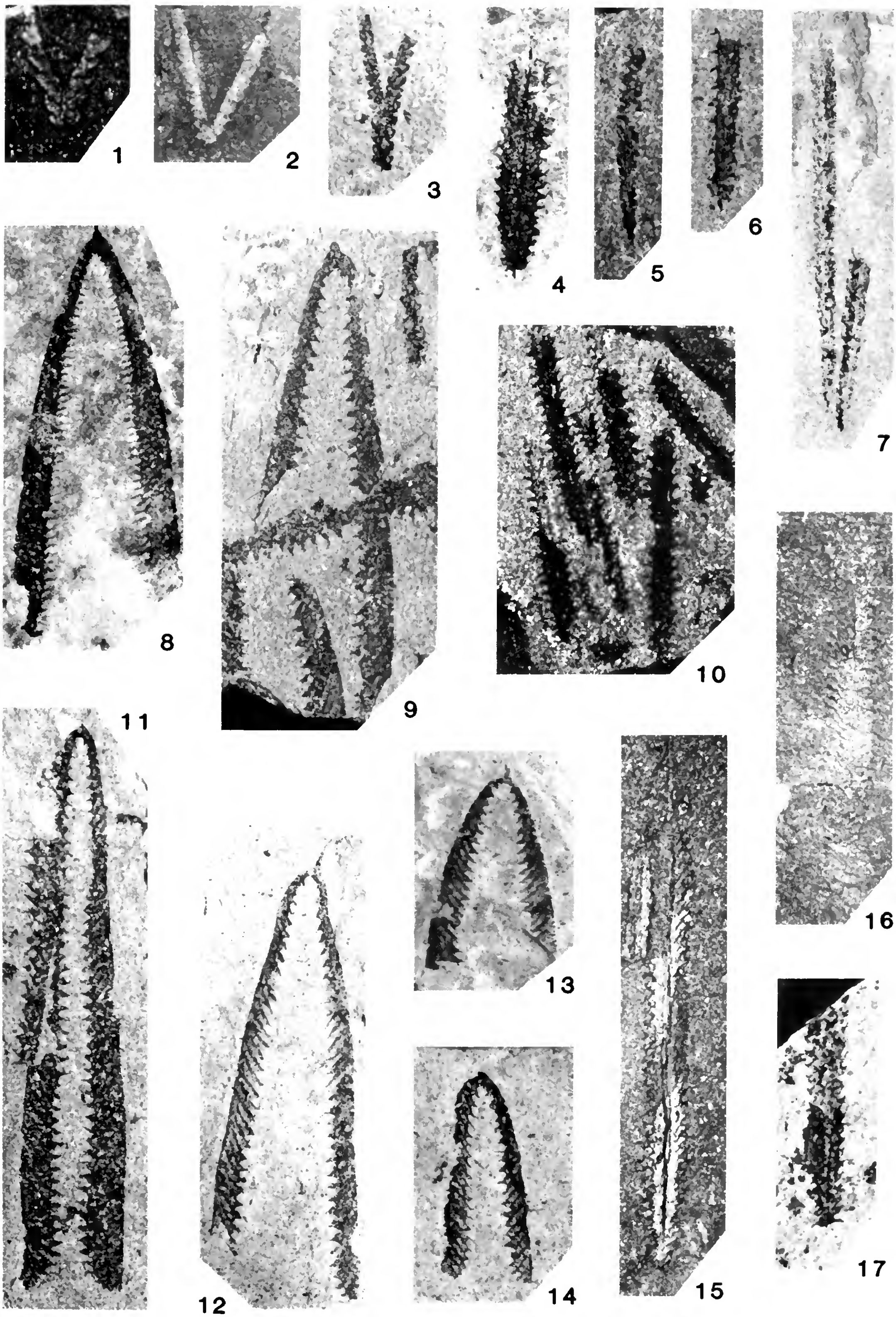
cf. 1876 *Corynoides curtus* Lapworth: pl. 4, fig. 92.
cf. 1949 *Corynoides curtus* Lapworth; Strachan: 157, text-figs 2a–g.

DESCRIPTION. Rhabdosome 6–8 mm long, 0·6 mm wide, consisting of a long sicula and one or two thecae, all poorly preserved.

DISCUSSION. A single slab of Aldress Shales (Q.5262, Loc. 355) is crowded with specimens which are clearly *Corynoides* associated with *Climacograptus*. They agree in size with *C. curtus*, rather than *C. calicularis* which is considerably longer. Riva (1974) suggested that the two forms should be regarded as the same but he has clearly misunderstood the characters of the genus and the differences in aspect between the two forms. Since Ruedemann's (1947) figures of American material are apparently unreliable (*fide* Riva 1974: 37), further work is necessary beyond the comparisons which I made in 1949. It seems unwise to restrict *C. americana* Ruedemann to forms which have only one fully-developed theca since the specimens in one swarm are often juveniles at the same stage of development.

PLATE 3 Figs 1–7 from Meadowtown Member; Figs 8–12, 15–17 from Betton Member; Figs 13, 14 from Weston Member.

Fig. 1 *Dicranograptus irregularis* Hadding, p. 32. Q.5286, Loc. 144. ×6. See also Text-fig. 29, p. 33.
Fig. 2 *Dicellograptus sextans* (Hall), p. 29. Q.5272, Loc. 324. ×3. See also Text-fig. 22, p. 30.
Fig. 3 *Dicranograptus* sp., p. 34. Q.5292, Loc. 314. ×3.
Fig. 4 *Diplograptus foliaceus* (Murchison), p. 34. Q.5293, Loc. 563. ×3. See also Pl. 6.
Fig. 5 *Climacograptus* cf. *brevis* Elles & Wood, p. 42. Q.5329, Loc. 314. ×3. See also Pl. 5.
Fig. 6 *Cryptograptus schaeferi* Lapworth, p. 25. Q.5261, Loc. 503. ×3.
Fig. 7 *Climacograptus* aff. *antiquus lineatus* Elles & Wood, p. 41. Q.5325, Loc. 957A. ×3. See also Pl. 6.
Figs 8, 9 *Didymograptus murchisoni* (Beck), p. 12. Fig. 8, BU.2080 (E. M. R. Wood collection), Holywell Brook. ×2. Fig. 9, Q.5209, Loc. 382A. ×3.
Fig. 10 *Gymnograptus* (?) sp., p. 47. Q.5338, Loc. 234. ×3. See also Text-fig. 39, p. 47.
Figs 11–14 *Didymograptus murchisoni* (Beck), p. 12. Fig. 11, Q.5210, Loc. 307. Fig. 12, Q.5211, Loc. 437. Fig. 13, Q.5212, stream junction W of Lyde. Fig. 14, Q.5213, Loc. 444. All ×3.
Figs 15, 16 *Gymnograptus* (?) sp., p. 47. Betton Dingle. Fig. 15, BU.2081 (Lapworth Collection). Fig. 16, BU.2082 (J. T. Wattison Collection). See also Text-fig. 40, p. 47. Both ×3.
Fig. 17 *Diplograptus foliaceus* (Murchison), p. 34. Q.5294, Loc. 575A. ×3. See also Pl. 6.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Family **NEMAGRAPTIDAE** Lapworth, 1873

Genus ***NEMAGRAPTUS*** Emmons, 1855

TYPE SPECIES. *Graptolithus gracilis* Hall 1848.

Nemagraptus gracilis (Hall 1847)
Pl. 4, fig. 8

1847 *Graptolithus gracilis* Hall: 274; pl. 74, figs 6a–d.
1903 *Nemagraptus gracilis* (Hall) Elles & Wood: 127; pl. 19, figs 1a–f; text-figs 76a–c.
1977 *Nemagraptus gracilis* (Hall); Finney: 121.

DISCUSSION. This widely recorded species and its varieties have been discussed in some detail by Finney (1977) but I cannot agree with him that the various appearances of the different forms are entirely due to differences of preservation of a single form. The Shelve specimens, although well preserved, are not easy to study since most are fragmentary and not exposed on single bedding planes. The typical S-shape of the rhabdosome is often clearly shown and the secondary stipes appear to arise from successive thecae of the primary stipes. The width of the branches seems to be never more than 0·4 mm while the primary stipes are only 0·3 mm. Most of the specimens are at least in semi-relief, which would account for their relative narrowness.

MATERIAL AND HORIZON. The species is widespread in the Rorrington Member but does not occur in either the beds above or below. Q.5263, Loc. 371; Q.5265, Loc. 594; Q.5266, Loc. 956.

A single specimen (Q.5264, Loc. 493) from the Rorrington Member shows much more widely spaced branches and may be referable to *N. gracilis distans* Ruedemann, but it is too incomplete for real determination (Pl. 4, fig. 4).

Genus ***LEPTOGRAPTUS*** Lapworth, 1873

TYPE SPECIES. *Graptolithus flaccidus* Hall 1865

Leptograptus validus Elles & Wood 1903
Pl. 4, figs 7, 9

1903 *Leptograptus validus* Lapworth MS; Elles & Wood: 113; pl. 16, figs 1a–e; text-figs 68a, b.

DESCRIPTION. Stipes often long, more than 10 cm long, but comparatively slender, the maximum width being 1·0 mm when compressed. The initial width of the stipes is about 0·4 mm and the increase is slow so that the stipes frequently only measure 0·7–0·8 mm wide in the distal parts. The sicula is generally prominent and is about 1·3 mm long. The first two thecae grow obliquely downwards and outwards from the level of the sicular aperture, so that it is generally hidden and there is only occasionally any sign of a virgella. The stipes then grow slightly upwards so that the later thecae are horizontal. There are no spines on the proximal thecae and the ventral walls of the later thecae are straight. The thecae number 10 to 12 per cm.

DISCUSSION. This Lapworth manuscript species was described by Elles & Wood as being abundant in the beds above the *Nemagraptus* Beds in Spy Burn and thus appears to be the form which Lapworth regarded as characterizing his 'Leptograptus Beds'. The species occurs commonly in the Rorrington Member and most of the localities in Whittard's collection yield *Nemagraptus* as well, e.g. Loc. 352. The few localities without *Nemagraptus* (e.g. Locs 373 and 374) are in what Whittard regarded as the highest part of the Rorrington Member, but are apparently succeeded by another locality, Loc. 371, in which both *L. validus* and *N. gracilis* occur. It is therefore doubtful if Lapworth's division of the Rorrington Flags into *Nemagraptus* and *Leptograptus* horizons can be maintained as a stratigraphic sequence.

MATERIAL AND HORIZON. Rorrington Member: Q.5267, Loc. 352; Q.5268, Loc. 374; Q.5263, Loc. 371.

Leptograptus latus Elles & Wood 1903
Pl. 5, fig. 4

1903 *Leptograptus latus* Elles & Wood: 116; pl. 16, figs 5a–e; text-figs 71a, b.

LECTOTYPE. Specimen GSM 49763 (British Geological Survey), figured by Elles & Wood (1903: pl. 16, fig. 5c), is here selected as being the best of the original figured specimens and the one which was also figured as text-fig. 71a.

DISCUSSION. This species has not been found in the Whittard Collection although it was originally described from the Shelve area, Rorrington Member. It is characterized by the more rapid widening of the stipes from an initial 0·4 mm to over 1 mm distally and the greater number of thecae, 12 to 14 per cm when compared with *L. validus*. It is included here for completeness.

Family **DICRANOGRAPTIDAE** Lapworth, 1873

Genus ***DICELLOGRAPTUS*** Hopkinson, 1871

TYPE SPECIES. *Didymograpsus elegans* Carruthers 1867.

Dicellograptus divaricatus (Hall 1859)
Pl. 4, fig. 1

1859 *Graptolithus divaricatus* Hall: 513; figs 3, 4.
1904 *Dicellograptus divaricatus* (Hall); Elles & Wood: 143; text-figs 87b, c.

DESCRIPTION. Stipes up to several cm long, diverging from a rounded axil at 50° to 70°, slender at first (0·6 mm) but widening in the first 10 mm to about 1 mm which is then maintained. Thecae about 11 per cm, with curved ventral walls, apertures opening into deep excavations which occupy up to half the width of the stipe and two-fifths of the free ventral length of the thecae. The first few thecae on each stipe bear prominent mesial spines but later thecae have only slightly curved supragenicular walls.

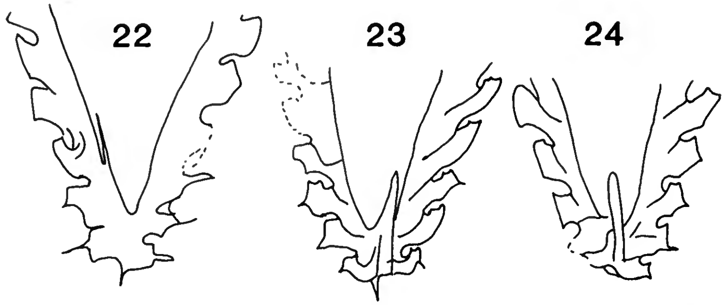
DISCUSSION. Hall's original description of this species (1859) included a wide range of axial angle and stipe curvature but later workers have generally accepted the restriction of the species to forms with straight stipes diverging at about 60°–70°. Hall (1865: 14) later notes that *D. sextans* differs in having the branches united for the first pair of thecae, while in *D. divaricatus* the branches are entirely separate. This, however, is not quite so clear when typical specimens are examined. In both forms, the sicula is generally incorporated into one of the stipes, leading to a compact proximal end. The axil in *D. divaricatus*, however, always seems to be more rounded.

MATERIAL AND HORIZONS. A single specimen, Q.5270, has been found in the Meadowtown Member, Loc. 164, and the species also occurs in the Rorrington Member (Q.5269, Loc. 497; Q.5271, Loc. 390) but it is not common. Elles & Wood recorded it doubtfully from Spy Burn, a stream which exposes a section from Betton Member to Aldress Member, but their other records from Spy Burn include *Didymograptus superstes* and *Nemagraptus gracilis* so it appears that the Rorrington Member is the horizon intended.

Dicellograptus sextans (Hall 1847)
Figs 22–24; Pl. 3, fig. 2; Pl. 4, fig. 2

1847 *Graptolithus sextans* Hall: 273; pl. 74, fig. 3.
1904 *Dicellograptus sextans* (Hall); Elles & Wood: 153; pl. 21, figs 1a–c; text-figs 96a, b.

DESCRIPTION. Stipes generally up to 1 cm long but may reach 2·5 cm, diverging at 40° to 60°, straight; width 0·6 mm at proximal end but widening rapidly to 0·8 or 0·9 mm which is then maintained; thecae about 12 per cm, occasionally closer; proximal two or three on each stipe



Figs 22–24 *Dicellograptus sextans* (Hall). Fig. 22, Q.5272, Loc. 324. Proximal part of Pl. 3, fig. 2, showing sicula almost totally incorporated in the second stipe. Fig. 23, Q.5273, Loc. 377. Sicula partially incorporated. Fig. 24, Q.5274, Loc. 497. Proximal part of Pl. 4, fig. 2 showing the free sicula. All × 10.

with stout mesial spines, later thecae simply with convex ventral walls becoming straight distally; apertures introverted, opening into deep and fairly wide excavations occupying about half the width of the stipe and a quarter of the total length of the thecae. The position of the sicula is variable, being free, more or less inclined or even incorporated into one stipe. Its length is about 1·5 mm and there is a prominent but short virgella.

Discussion. In the absence of any modern redescription of Hall's species, I have taken forms similar to those figured by Elles & Wood as being typical of the species. The main differing feature of the Shelve specimens is the appearance of the sicula. Elles & Wood (1904) give its length as 0·7 mm and say that it never appears conspicuously in the axil. The two specimens figured here showing the sicula in the axil have all the other characters of *D. sextans* (and of no other described form). The length of the sicula agrees with at least one of the specimens figured by Elles & Wood although it is not easy to obtain the exact figure when the apex of the sicula is incorporated into a stipe.

Material and horizons. Rorrington Member: Q.5273, Loc. 377; Q.5274, Loc. 497. Topmost Meadowtown Member: Q.5272, Loc. 324; Q.5275, Loc. 164.

Dicellograptus intortus Lapworth 1880
Fig. 25; Pl. 4, fig. 3

1880 *Dicellograptus intortus* Lapworth: 161; pl. 5, fig. 19a.
1904 *Dicellograptus intortus* Lapworth; Elles & Wood: 146; pl. 20, figs 4a–f; text-figs 90a–d.

Description. The proximal end of this species shows considerable variation in appearance in differing views. The stipes are twisted distally but rarely show crossing of the stipes (cf. Williams 1981). The whole rhabdosome, however, is occasionally found in a side view with the stipes more or less overlapping. Stipes up to 18 mm long, initial width 0·4 mm, widening steadily to a maximum of about 0·8 mm. The axillary angle is small, 20° to 25°, and the first two pairs of thecae form a compact proximal end approaching the dicranograptid state. The proximal four or five thecae on each stipe bear stout mesial spines and the apertures open into deep excavations. Owing to the twisting of the stipes, profile views of the distal thecae are rare.

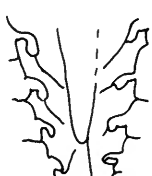


Fig. 25 *Dicellograptus intortus* Lapworth. Q.5276, Loc. 390. Enlargement of proximal part of Pl. 4, fig. 3, × 10.

DISCUSSION. Erdtmann (1976) has put *D. smithi* Ruedemann into synonymy with *D. intortus*, but the latter seems to have fewer spined thecae. Obut & Sobolevskaya (1964: pl. 5, fig. 2) figure a specimen as *D. intortus*, but it again seems to have mesial spines on fairly distal thecae. Clearly much further study of these forms is required.

MATERIAL AND HORIZONS. The species is common at a few localities in the Rorrington Member: Q.5276, Loc. 390; Q.5278, Loc. 389; Q.5355, Loc. 374. A single specimen, Q.5277, attributed to this species, occurs in the succeeding Spy Wood Member, Loc. 394.

Dicellograptus salopiensis Elles & Wood 1904
Fig. 26; Pl. 4, fig. 6

1904 *Dicellograptus divaricatus* var. *salopiensis* Elles & Wood: 145; pl. 20, figs 7a–c, e; text-figs 89a, b.

DESCRIPTION. Stipes up to 2 cm long, with a constant width of 0·6 mm, diverging at 60° to 80°; thecae 14 to 12 per cm, with curved ventral walls, the proximal thecae bearing stout mesial spines; apertures opening into deep but narrow excavations which occupy about a quarter of the length of the theca. Sicula 1·8 mm long, incorporated into the second stipe, virgella prominent.

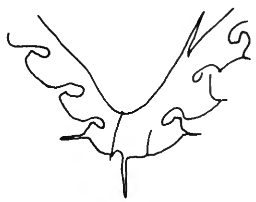


Fig. 26 *Dicellograptus salopiensis* Elles & Wood. Q.5279, Loc. 479. Enlargement of proximal part of Pl. 4, fig. 6, × 10.

DISCUSSION. Elles & Wood distinguished this form as a variety of *D. divaricatus* on its more slender stipes. It has been much more widely recorded by later workers than *D. divaricatus* itself and seems worthy of recognition as a full species, pending a complete review of the genus. The subdivision into four groups by Elles & Wood cannot be used when *salopiensis* as a variety of *divaricatus* is in a different group from *sextans*, whose variety *exilis* is very close to *salopiensis* (see below).

MATERIAL AND HORIZON. *D. salopiensis* is widely distributed in the Rorrington Member (e.g. Q.5279, Loc. 479) but is not common at any locality.

Dicellograptus exilis Elles & Wood 1904
Pl. 4, fig. 5; Pl. 5, fig. 13.

1904 *Dicellograptus sextans* var. *exilis* Elles & Wood: 155; pl. 21, figs 2a–d; text-fig. 97.

DESCRIPTION. Stipes up to 3·5 cm, straight, diverging at 30° to 50°, width almost uniform, 0·3–0·5 mm. Thecae 13 to 14 per cm, the first four or five on each stipe bearing mesial spines. Sicula apparently incorporated into one stipe.

DISCUSSION. Erdtmann (1976) has put *exilis* into synonymy with *salopiensis* but the two forms seem to be distinct in the Shelve area, *D. exilis* being distinguished by its narrower stipes and narrower axil.

MATERIAL AND HORIZONS. Specimens referred to *D. exilis* are rare in the Rorrington Member (Q.5280, Loc. 493), and a single specimen has been found in the succeeding Spy Wood Member (Q.5281, loc. unknown).

Dicellograptus cf. ***vagus*** Hadding 1913

cf. 1913 *Dicellograptus vagus* Hadding: 53; pl. 4, figs 15–19.

DESCRIPTION. Stipes 17 mm long, width almost uniform, 0·6–0·7 mm; thecae 13 per cm, similar to those of *D. sextans*. Stipes diverging at 25°.

DISCUSSION. A single specimen (Q.5282) from the Meadowtown Member (Loc. 503) appears to be fairly close to *D. vagus* although the sicula is not conspicuous. The specimen is poorly preserved but the stipes do not seem to show the twisting characteristic of *D. intortus*. The occurrence of three different forms of *Dicellograptus* in the Meadowtown Member is interesting. Toghill (1970) has described *D.* cf. *vagus* from the Hendre Shales of south Wales on the same horizon as at Shelve and Berry (1964) figured it from Norway, but in both cases no other species of *Dicellograptus* is recorded from the same horizon.

Genus *DICRANOGRAPTUS* Hall, 1865

TYPE SPECIES. *Graptolithus ramosus* Hall 1847.

Elles & Wood (1904) subdivided the genus into four groups based on distal thecal characters, but examination of some of their figured specimens does not uphold some of the distinctions. As with *Dicellograptus*, it seems best to leave the genus undivided until the species all receive modern critical re-examination.

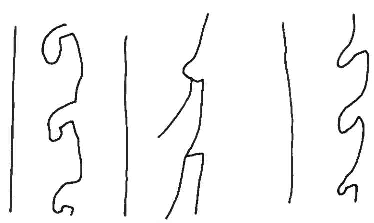
Dicranograptus brevicaulis Elles & Wood 1904
Fig. 27; Pl. 5, fig. 2

1904 *Dicranograptus brevicaulis* Elles & Wood: 168; pl. 24, figs 3a–d, text-fig. 105.

DESCRIPTION. Biserial portion very short, about 3 mm long, consisting of 4 or 5 pairs of thecae and widening from 0·8 mm to 1·6 mm at the axil. Branches uniformly 0·8 mm wide, diverging at 25° to 30° and 25 mm or more long. Proximal thecae apparently all spined up to the base of the branches. Thecae 14 to 12 per cm, apertures introverted, opening into deep excavations.

DISCUSSION. The main distinguishing feature of *D. brevicaulis* from the accompanying *D. rectus* appears to be the length of the biserial portion, although the spines seem to be less well developed in *brevicaulis*. Their appearance, however, is very dependant on the state of preservation and specimens in full relief (?pyritic internal casts) show few traces of spines.

MATERIAL AND HORIZON. The species is fairly widespread in the Rorrington Member and is common at a few localities, e.g. Q.5284, Loc. 334; Q.5285, Loc. 371; Q.5283, Loc. 374.



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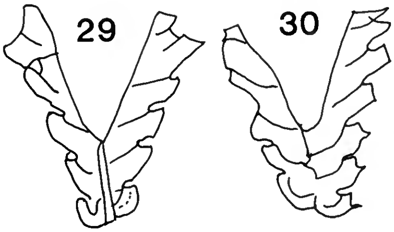
Figs 27, 28 *Dicranograptus* spp., uniserial stipes. Fig. 27, *D. brevicaulis* Elles & Wood. a, proximal and b, distal parts of Q.5284, Loc. 334, showing variation in appearance. Fig. 28, *D. rectus* Hopkinson. Q.5289, Loc. 956. Enlargement of part of Pl. 5, fig. 1. All × 10.

Dicranograptus irregularis Hadding 1913
Figs 29, 30; Pl. 3, fig. 1

1913 *Dicranograptus irregularis* Hadding: 52; pl. 4, figs 1–12.

DESCRIPTION. Biserial portion very short, about 1 mm long, consisting of 2 or 3 pairs of thecae which are markedly alternate. The width increases from about 1 mm to 1·5 mm where the uniserial stipes diverge at an angle of 40° to 60°. These are up to 6 mm long and have a breadth of 0·6–0·8 mm. Thecae are closely spaced, about 16 per cm, and have slightly introverted apertures opening into narrow excavations. The sicula appears to be the full length of the biserial portion and is exposed for the whole of the obverse view in several specimens.



Figs 29, 30 *Dicranograptus irregularis* Hadding. Fig. 29, obverse view showing sicula, Q.5286. Fig. 30, reverse view, Q.5287. Both Loc. 144, ×10.

DISCUSSION. Hadding's enlarged figures show spines on only the basal pair of thecae at most, but the Shelve material shows a greater development of spines; in a few specimens all the thecae bear spines.

MATERIAL AND HORIZON. The species is rare and is confined to the Meadowtown Member: Q.5286, Q.5287, Loc. 144; Q.5288, Loc. 324; Q.5357, Loc. 503.

Toghill (1970) has figured a possible specimen of the species from the Hendre Shales and Berry (1964) has described specimens from Norway from the *Didymograptus murchisoni* Zone, marginally earlier than the Shelve occurrence.

Dicranograptus rectus Hopkinson 1872

Fig. 28; Pl. 5, figs 1, 3, 11

1872 *Dicranograptus rectus* Hopkinson: 508; pl. 12, fig. 10.
1904 *Dicranograptus rectus* Hopkinson; Elles & Wood: 169; pl. 24, figs 4a–e; text-figs 106a, b.

DESCRIPTION. Biserial portion short, about 5 mm long, consisting of 7 or 8 pairs of thecae and widening from 0·8 mm at the proximal end to 2·0 mm at the axil. Uniserial branches up to 10 cm long or more, diverging at 25° to 30°, with a uniform width which varies from 0·6 mm to 1·0 mm depending on the state of preservation. Thecae closely set on the biserial portion (15 per cm) but more widely spaced on the branches (10 per cm). All the biserial thecae bear prominent mesial spines and these are also seen on the first few thecae of the branches. The more distal thecae appear to have straight ventral walls and the thecal apertures open into deep excavations.

DISCUSSION. The species is distinguished by the comparatively short biserial portion which is also very spiny and by the fact that the ventral margin of each branch forms nearly a straight line with the biserial portion. This was Hopkinson's original criterion by which he distinguished *rectus* from his earlier-described *D. nicholsoni*. In the original description Hopkinson gives the length of the biserial portion as $\frac{1}{10}$ to $\frac{1}{5}$ of an inch (2·5–5 mm), but Elles & Wood give this figure as 6–8 mm, presumably putting the shorter forms into their new species *D. brevicaulis*. One of their figured specimens of *D. brevicaulis* (1904: pl. 24, fig. 3b) is at any rate originally labelled *D. rectus* and would appear to be better placed there. Elles & Wood, however, put the two species into different groups of the genus, based on the distal thecal shape, but examination of some of the figured material does not substantiate the criteria for separating the groups. The apertures in both *D. brevicaulis* and *D. rectus* are strongly introverted, opening into deep pouch-like excavations. The difference between the species then appears to be mainly the length of the biserial portion, but there are not enough specimens in the present material to provide any real measure of the range present. Other short-stemmed species such as *D. hians* T. S. Hall can be distinguished by the much greater angle of divergence of the branches.

MATERIAL AND HORIZONS. *D. rectus* is a rare species occurring in the Rorrington Member: Q.5289, Loc. 956; Q.5290, Loc. 373. One specimen has been found in the succeeding Spy Wood Member: Q.5291, Loc. 417A.

Dicranograptus sp.
Pl. 3, fig. 3

A single specimen, Q.5292, from the Meadowtown Member, Loc. 314, has a biserial portion 4 mm long with a width of 1·0–1·6 mm, and short (6 mm) branches which are 0·8 mm wide. Thecae number about 15 per cm. The first two thecae show traces of spines, but none of the later thecae have them although the preservation ought to show them if present. In general dimensions and shape it is similar to *D. rectus* but the absence of spines precludes that species. It is also similar to *D. clingani* but the horizon is far too low for that species. There are traces of a structure (?virgula) between the two branches, and it is possible that the specimen is a split diplograptid such as has been found in the Lower Silurian (Williams 1983: text-fig. 3b).

Family **DIPLOGRAPTIDAE** Lapworth, 1873

Genus ***DIPLOGRAPTUS*** M'Coy, 1850

TYPE SPECIES. *Graptolithus foliaceus* Murchison 1839.

Diplograptus foliaceus (Murchison 1839)
Pl. 3, figs 4, 17; Pl. 6, figs 10, 11

1839 *Graptolithus foliaceus* Murchison: 694; pl. 26, figs 3, 3a.
1907 *Diplograptus* (*Mesograptus*) *foliaceus* (Murchison); Elles & Wood: 259; pl. 31, figs 8a–f, text-figs 177a–d.

DESCRIPTION. Rhabdosome up to 3 cm long, widening from 0·8–1·0 mm at th1^1 to 1·6–2·0 mm at 5 mm, and to a maximum of about 3·0 mm. Thecae usually 8 to 9 in the first 5 mm, 12 to 14 per cm distally, proximal thecae climacograptid with rather shallow excavations occupying up to a quarter of the width of the rhabdosome and a third of the free ventral edge, distal thecae becoming orthograptid after about the first 10 mm, th1^1 and 1^2 with subapertural spines; virgella slender.

DISCUSSION. Elles & Wood (1907) commented on the confusion that surrounded this name in the 19th century and provided the first good account. It is surprising, therefore, that they did not give any good comparison with their new species *D. multidens*, simply implying that the latter was broader and had more numerous thecae. Re-examination of the illustrations and specimens of *foliaceus* shows that its proximal thecal count is as high as that for *multidens*, so that it is only the larger size of the latter which distinguished it. This may account for the lack of references to *D. foliaceus*, as most forms with a high thecal count at this horizon have been

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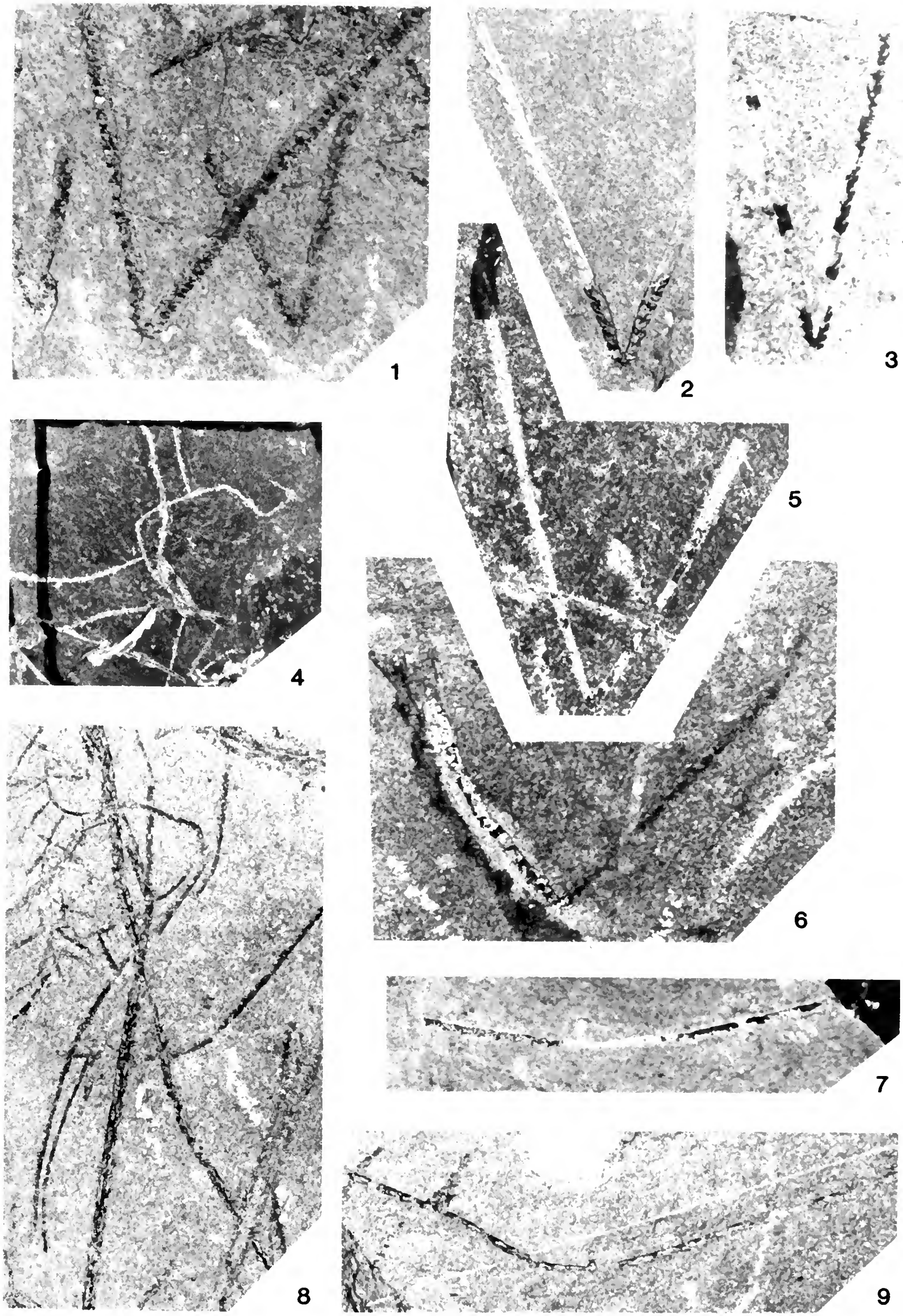
PLATE 4 All specimens from the Rorrington Member.

Fig. 1 *Dicellograptus divaricatus* (Hall), p. 29. Q.5269, Loc. 497. ×3.
Fig. 2 *Dicellograptus sextans* (Hall), p. 29. Q.5274, Loc. 497. ×3. See also Text-fig. 24, p. 30.
Fig. 3 *Dicellograptus intortus* Lapworth, p. 30. Q.5276, Loc. 390. ×3. See also Text-fig. 25, p. 28.
Fig. 4 *Nemagraptus gracilis* cf. *distans* Ruedemann, p. 31. Q.5264, Loc. 493. ×1.
Fig. 5 *Dicellograptus exilis* Elles & Wood, p. 31. Q.5280, Loc. 493. ×3.
Fig. 6 *Dicellograptus salopiensis* Elles & Wood, p. 31. Q.5279, Loc. 479. ×3. See also Text-fig. 26, p. 31.
Fig. 7 *Leptograptus validus* Elles & Wood, p. 28. Q.5267, Loc. 352. ×3.
Fig. 8 *Nemagraptus gracilis* (Hall), p. 28. Q.5263, Loc. 371. ×3.
Fig. 9 *Leptograptus validus* Elles & Wood, p. 28. GSM 99759, Spy Burn. ×3.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called *multidens* (e.g. Bulman 1948). The type locality for *D. foliaceus* is in the Meadowtown Member. It does not seem to occur in the more shaly Rorrington Member but reappears in the Chirbury Formation and is found to the highest beds in the Shelve area.

MATERIAL AND HORIZONS. ?Betton Member: Q.5294, Loc. 575A. Meadowtown Member: Q.5293, Loc. 563. Whittery Member: Q.5295, Loc. 299; Q.5296, Loc. 294. Hagley Member: Q.5358, Loc. 739.

Diplograptus leptotheca Bulman 1946
Pl. 6, figs 1, 3, 4, 13

1946 *Diplograptus leptotheca* Bulman: 43; pl. 4, figs 1–15, pl. 6, fig. 11; text-figs 21–23.

DESCRIPTION. Rhabdosome up to 2 cm long, widening from 0·8–1·0 mm at th1^1 to 1·4–1·6 mm at 5 mm and reaching 1·8–2·0 mm distally. Thecae 18 to 14 per cm, proximal thecae with a well-marked excavation occupying a quarter of the width of the rhabdosome and a third to a half of the free ventral edge, distal thecae becoming orthograptid.

DISCUSSION. Some specimens which widened rather more rapidly were originally identified as *D. compactus* Elles & Wood, but none attain a width of more than 2·0 mm (*D. compactus* reaches 3·0 mm), and it seems preferable to call them all by the same name. This species was originally described from isolated material from Girvan and in dimensions is very similar to *D. diminutus* Ruedemann 1947 *non* Elles & Wood 1907. The American species has been figured from Kazakhstan by Tzaj (1976) and his figure is very like *D. leptotheca.*

MATERIAL AND HORIZONS. The species occurs fairly commonly in the Aldress Member; Q.5298, Q.5299, Loc. 302; Q.5297, Loc. 304; also in the succeeding parts of the Chirbury Formation, e.g. Hagley Member; Q.5300, Loc. 744. A single specimen, Q.5301, has been noted from the earlier Rorrington Member, Loc. 334, associated with *N. gracilis.*

Diplograptus multidens Elles & Wood 1907

1907 *Diplograptus* (*Mesograptus*) *multidens* Elles & Wood: 261; pl. 31, figs 9a–d, text-fig. 178.

DESCRIPTION. Rhabdosome 2·5 cm long, widening from 1·4 mm at the proximal end to 4·0 mm distally. Thecae 19 to 14 per cm, proximal ones amplexograptid but rapidly becoming orthograptid.

DISCUSSION. Only a single specimen (Q.5302) from the Aldress Member (Loc. 343) agrees with the dimensions of this species, whose type locality is at Pontesford, just to the north-east of the Shelve area. There are, however, a considerable number of smaller specimens with the same high thecal count which are now put with *D. foliaceus.* The contrast with the Oakwood Shales of Pontesford is striking, since there almost all the diplograptids show widths of more than 3 mm. The specimens from Shelve figured by Bulman (1948) as *D. multidens* I would regard as *D. foliaceus* on account of their width.

Genus *AMPLEXOGRAPTUS* Elles & Wood, 1907

TYPE SPECIES. *Diplograptus perexcavatus* Lapworth 1876.

Amplexograptus cf. *confertus* (Lapworth 1875)
Pl. 2, fig. 9

cf. 1875 *Climacograptus confertus* Lapworth: 655; pl. 34, figs 4a–f.
cf. 1907 *Diplograptus* (*Amplexograptus*) *confertus* (Lapworth); Elles & Wood: 269; pl. 31, figs 18a–c, text-figs 185a–c.

DESCRIPTION. Rhabdosome about 10 mm long, widening from about 0·8–1·0 mm at th1^1 to 1·6 mm. Thecae 16 per cm, with deep excavations occupying about a quarter of the width of the rhabdosome and half of the ventral margin.

Discussion. This species is possibly represented by two specimens in the collection, one from the Hope Member (Q.5303, Loc. 959) and the other from the Stapeley Member (Q.5304, Loc. 946). Neither specimen is very well preserved. The species has been used as a zonal index in China for the lower part of the Llanvirn.

Amplexograptus fallax Bulman 1962
Fig. 31

1962 *Amplexograptus fallax* Bulman: 463; text-figs 2A–E.

Description. Rhabdosome up to 1·5 cm long, widening from 1·0 mm at th1[1] to 1·8 mm in the first 5 mm, then remaining uniform. Thecae 16 to 14 per cm, with deep and wide excavations occupying a quarter of the width of the rhabdosome and a third to a half of the free ventral edge; supragenicular wall distinctly inclined outwards. Th1[1] with a subapertural spine. Virgella short.

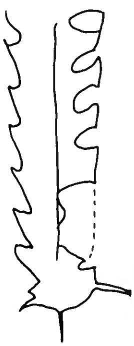


Fig. 31 *Amplexograptus fallax* Bulman. Q.5305, Loc. 346. × 10.

Discussion. Two specimens from the Aldress Member match this species, but the preservation is not very good. Other specimens from higher horizons occasionally show thecae approaching the amplexograptid type but these can probably be accommodated in the various climacographtids which occur there and which show considerable range of thecal form depending on the preservation.

Material and horizon. Aldress Member: Q.5305, Loc. 346; Q.5306, Loc. 318.

Genus *GLYPTOGRAPTUS* Lapworth 1873

Type species. *Diplograpsus tamariscus* Nicholson 1868.

Glyptograptus dentatus (Brongniart 1828)
Pl. 1, fig. 12; Pl. 2, fig. 10

1963 *Glyptograptus dentatus* (Brongniart); Bulman: 673; pl. 96, figs 1–5; text-figs 1, 4 (with full synonymy).

Description. Rhabdosome up to 2 cm long, widening from 0·5–0·8 mm at th1[1] to 1·8–2·0 mm in the first 10 mm, thereafter almost uniform. Thecae 8 to 9 in the first 5 mm, 6 to 7 in 5 mm distally, the first two thecae usually with short apertural spines. Virgella fairly stout.

Discussion. A number of biserial forms occur in the Hope Member and some (e.g. Q.5308, Loc. 701) agree fairly well with the revised description of *G. dentatus* given by Bulman (1963). They are, however, not well preserved. A single specimen with similar characters occurs in the Mytton Member (Q.5307, Loc. 905) associated with horizontal didymograptids and seems reasonably distinct from the common diplograptid found at Shelve Church. Chen (1982) has described a number of new forms from China and Paškevičius (1981) has also described new glyptograptids. The early Shelve material is not abundant enough nor well enough preserved to allow comparisons.

Glyptograptus shelvensis Bulman 1963
Pl. 1, fig. 10

1963 *Glyptograptus shelvensis* Bulman: 676; pl. 97, figs 1–3, 14, text-figs 5a–f.

Bulman described this species as a small form of *G. dentatus*, and also described other specimens from the Mytton Member at Shelve Church under the names *G. austrodentatus anglicus* and *G. a. mutabilis*. Jenkins (1980) figured four specimens of these forms and claimed that they simply showed the effects of distortion on a single species. Apart from his text-figure caption being wrong (his sequence A to D should be reversed and his fig. 3C is *mutabilis* not *anglicus*), I do not think that he has fully considered the problem of compression of a three-dimensional object, and, although perhaps Bulman's forms are too restricted in range of variation, it is unwise to assume that only one form is present. Certainly there is no evidence that I have seen from Shelve Church specimens (e.g. BU.2076) to suggest that they should be put into the genus *Undulograptus* as Jenkins claims. There is considerable variation in thecal shape which is consistent with differing views of the rhabdosome. This is a common feature of the Shelve Inlier specimens, which are frequently preserved in some relief, and at Shelve Church in particular this apparent variation has been increased by tectonic deformation. The Whittard collection does not add enough to Bulman's original work for further comment at present.

Glyptograptus teretiusculus (Hisinger 1840)
Fig. 32; Pl. 5, fig. 10

1840 *Prionotus teretiusculus* Hisinger: 5; pl. 38, fig. 4.
1907 *Diplograptus* (*Glyptograptus*) *teretiusculus* (Hisinger); Elles & Wood: 250; pl. 31, figs 1a–e, text-figs 171a–d.

DESCRIPTION. Rhabdosome up to 2 cm long, widening from 1·0 mm at $th1^1$ to 1·6 mm in the first 10 mm, thereafter widening only a little. Thecae 14 to 12 per cm of simple glyptograptid type, the first two thecae bearing short spines. Virgella long, 3·5 mm, and slender. Median septum apparently complete.

DISCUSSION. Only a few specimens (e.g. Q.5309, Loc. 375) can be safely attributed to this species, although some poorly preserved specimens may belong here. They occur in the Rorrington Member associated with *Nemagraptus*, *Leptograptus*, *Dicellograptus* and *Dicranograptus*, indicating the *N. gracilis* Zone. I originally identified a slender proximal end from the underlying Meadowtown Member as *G. teretiusculus*, but re-examination shows that the later thecae have distinct apertural lappets and I now regard it as more like *Orthograptus uplandicus*. However, Bulman (1936: text-fig. 22) figured *G. dentatus–teretiusculus* transients with fairly clear apertural lappets, but there does not seem to be good isolated material from higher horizons which shows the real shape of the thecae.

Fig. 32 *Glyptograptus teretiusculus* (Hisinger). Q.5309, Loc. 375. Drawing of Pl. 5, fig. 10, ×5.

Glyptograptus sp.
Fig. 33; Pl. 2, fig. 12

DESCRIPTION. Rhabdosome 16 mm long, widening from 0·6 mm at th1^1 to 2·5 mm. The thecae number 16 to 14 per cm and there is a short, stout virgella. The proximal end is very pointed and there is no trace of spines on the first pair of thecae.

DISCUSSION. This specimen from the Hope Member (Q.5310, Loc. 959) has distal thecae of the glyptograptid type, but the proximal end is quite unlike the contemporary *G. dentatus* and seems to be much more advanced. The first pair of thecae grow upwards like those of *Climacograptus brevis* with very little outward growth. The early occurrence of this feature merits notice but a single specimen is inadequate for the erection of a new species.

Fig. 33 *Glyptograptus* sp. Q.5310, Loc. 959. Proximal part of Pl. 2, fig. 12, × 5.

Genus *ORTHOGRAPTUS* Lapworth, 1873

TYPE SPECIES. *Graptolithus quadrimucronatus* Hall 1865.

The genus is kept here undivided as although *Rectograptus* Přibyl 1950 (type *D. truncatus* Lapworth) is reasonably well characterized the relationships of the other groups recognized by Elles & Wood are not clear.

Orthograptus cf. *apiculatus* (Elles & Wood 1907)
Pl. 5, fig. 14

cf. 1907 *Diplograptus* (*Orthograptus*) *rugosus* Emmons var. *apiculatus* Elles & Wood: 245; pl. 30, figs 7a–d, text-figs 166a–e.
cf. 1946 *Orthograptus apiculatus* (Elles & Wood); Bulman: 51; pl. 5, figs 1–16; pl. 6, figs 1–7; text-figs 24–29.

DESCRIPTION. The proximal end is 0·8–0·9 mm wide and there are 6 to 7 thecae in the first 5 mm. The rhabdosome widens gradually over the first 2 cm and long specimens may show a slight reduction in width distally. The thecal apertures have the characteristic spreading appearance of the *calcaratus* group with slight apertural lappets distinguishing them from the *truncatus* type.

DISCUSSION. This species was redescribed from well-preserved material by Bulman (1946). The Shelve specimens are generally narrower than the Scottish material and specimens in relief reach only 2 mm width at 3 cm length. However, the other characters appear to agree well with *O. apiculatus* and are quite distinct from *O. uplandicus* which occurs in the same beds.

MATERIAL AND HORIZONS. Spy Wood Member: Q.5312, Loc. 333; Q.5311, Loc. 422. Aldress Member: Q.5313, Loc. 395.

Orthograptus calcaratus vulgatus (Elles & Wood 1907)
Pl. 6, figs 14, 16

1907 *Diplograptus* (*Orthograptus*) *calcaratus* var. *vulgatus* Elles & Wood: 241; pl. 30, figs 5a–d; text-figs 160a–d.

DISCUSSION. The highest beds in the Shelve Inlier yield numerous orthograptids of the *calcaratus* group. They show rapid widening from a proximal end of about 1·0 mm to a maximum of 2·8 or 3·0 mm, occasionally more, but they lack the stout proximal spines of the normal species. The proximal thecae number 7 in the first 5 mm, agreeing with some of the type material, although this figure is a good deal higher than the 10 to 8 per cm given by Elles & Wood. The intermediate value of 12 per cm is reported for the subspecies *acutus*, so it is probable that re-evaluation of all the forms is required. They may have some stratigraphical value if critically assessed, as *O. apiculatus* and *O. uplandicus* are also part of the complex.

MATERIAL AND HORIZONS. Hagley Member: Q.5315, Loc. 739. Whittery Member: Q.5314, Loc. 299.

Orthograptus truncatus (Lapworth 1877)
Pl. 6, figs 6, 15

1877 *Diplograptus truncatus* Lapworth: 133; pl. 6, fig. 17.
1907 *Diplograptus* (*Orthograptus*) *truncatus* Lapworth; Elles & Wood: 233; pl. 29, figs 3a–e; text-figs 154a, b.
1948 *Orthograptus truncatus* (Lapworth)?; Bulman: 226; text-fig. 3d.

A few specimens from the higher beds of the inlier show the characteristics of the *truncatus* group, simple straight thecae without paired apertural spines. Bulman (1948) has already figured a specimen from the Aldress Member as probably this species and Elles & Wood record it from Whittery Dingle, presumably in Whittery Member. Whittard's collection has produced only four specimens, two from the Aldress Member, Q.5316–7, Loc. 302, and two from the Whittery Member, Q.5318–9, Loc. 272. While not as wide as some *truncatus*, it must be remembered that these specimens are in at least partial relief where a maximum of 3 mm appears to be normal. The thecal count is higher than in Lapworth's Scottish specimens (8 or 9 in the first 5 mm as against 7) and this may reflect a real difference. However, the Shelve specimens agree better with the typical *truncatus* than with any of the varieties described by Elles & Wood and others.

Orthograptus uplandicus (Wiman 1895)
Fig. 34; Pl. 5, figs 6, 9, 12

1895 *Diplograptus uplandicus* Wiman: 274; pl. 9, fig. 1.
1963 *Orthograptus uplandicus* (Wiman); Geh: 248; pl. 4, fig. 7; text-fig. 10c.

DISCUSSION. This species, described from Sweden, appears to be an early slender representative of the *calcaratus* group. The initial width is slightly less than in *calcaratus* (0·8 mm instead of

Fig. 34 *Orthograptus uplandicus* (Wiman). BU.2083, Beyrichia Bed, Rorrington. Enlargement of part of Pl. 5, fig. 9, × 5.

1 mm) and the maximum breadth is only 2·6 mm while *calcaratus* frequently reaches 3 mm or more. The thecae have distinct lateral lappets, particularly on the proximal thecae, which give the impression of slight introversion of the aperture. The virgella is well developed in some specimens, providing a link with *calcaratus*. The thecae number 6 to 7 in the first 5 mm but only 5 in 5 mm distally, generally higher numbers than in *calcaratus* and its varieties as figured by Elles & Wood.

A young specimen from Hubei, China was figured by Geh (1963), which is the only other record of the species I have traced since its original description.

MATERIAL AND HORIZONS. Rorrington Member: Q.5320, Loc. 956; Q.5322, Loc. 413. Spy Wood Member: Q.5321, Loc. 333; Q.5323, Loc. 369. Aldress Member: Q.5347, Loc. 304.

Genus *CLIMACOGRAPTUS* Hall, 1865

TYPE SPECIES. *Graptolithus bicornis* Hall 1847.

Climacograptus cf. ***angustatus*** Ekström 1937
Pl. 2, fig. 14

cf. 1937 *Climacograptus angustatus* Ekström: 36; pl. 7, figs 1–6.
cf. 1964 *Climacograptus angustatus* Ekström; Berry: 132; pl. 13, figs 10, 12, 13.

A single specimen from the Hope Member (Q.5324, Illing Colln.) has the width and thecal number of this species although it is considerably longer, reaching a length of 35 mm. The thecal excavations seem to be larger than shown in Ekström's plate but agree with Berry's more detailed account. The specimen is clearly distinct from the other diplograptids in the Hope Member and shows no trace of the zigzag septum characteristic of *Pseudoclimacograptus*.

Climacograptus aff. ***antiquus lineatus*** Elles & Wood 1906
Pl. 3, fig. 7; Pl. 6, figs 1, 19, 20

DESCRIPTION. The rhabdosome is generally 15–20 mm long and widens from 0·6 mm to 1·5 mm, rarely reaching 1·8 or 1·9 mm. It is thus generally narrower than *lineatus* which, in the type specimen, reaches 2·0 mm. Details of the proximal end are usually poor but there is a short, stout virgella and the first two thecae bear short spines which appear to be subapertural. The thecae number 6 or 7 in the first 5 mm but only 11 per cm distally. The excavations are fairly deep, occupying a quarter or a third of the width of the rhabdosome and about a quarter of the ventral wall. The distal thecae frequently show inclined excavations but the proximal ones have horizontal apertures and a sharp geniculum.

DISCUSSION. These fairly numerous specimens of a comparatively slender climacograptid have the thecal characteristics of the *antiquus* type. Many are in relief and it is difficult to compare measurements, particularly width of rhabdosome and thecal excavations, with flattened type material. Pending a review of the relationships of Ordovician climacograptids, it seems unwise to propose further new names and these forms are here described under fairly open nomenclature.

The character of the proximal end clearly links them to *C. antiquus*, but they are much narrower and have generally more thecae. *C. macoris* Keller 1956 has the same width but the proximal end is quite different, as is that of *C. repetitus* Berry 1964. *C. yumenensis* Mu, Geh & Yin 1962 also lacks the paired thecal spines, although *C. shihuigouensis* var. *tricornis* Mu, Geh & Yin 1962 does have them. The latter, however, reaches a breadth of 2·3 mm although the normal form is only 1·5 mm wide. *C. antiquus lineatus* itself has been figured from China with a breadth of only 1·5 mm but the lower thecal count (8 to 11 per cm) (South Central Regional Atlas, see Wang *et al.* 1977). Hong (1957) had previously described *lineatus* from China with a breadth of at least 2 mm and 12 to 13 thecae per cm at the proximal end.

MATERIAL AND HORIZONS. The form is widely distributed in the Shelve area, ranging from the Meadowtown up to the Hagley Member. Meadowtown Member: Q.5325, Loc. 957A. Aldress Member: Q.5346, Loc. 302; Q.5326, Loc. 304. Hagley Member: Q.5327, Loc. 392A; Q.5328, Loc. 744.

Climacograptus brevis Elles & Wood 1906
Pl. 3, fig. 5; Pl. 5, figs 7, 8

1906 *Climacograptus brevis* Elles & Wood: 192; pl. 27, figs 2a–f; text-figs 125a, b.

This small species of *Climacograptus* occurs in some numbers at a few localities in the Rorrington (e.g. Q.5330, Loc. 519) and Aldress Members (e.g. Q.5353, Loc. 355; Q.5348, Loc. 343A), the latter, however, being very poorly preserved. The specimens range up to nearly 2 cm in length but with a maximum width of only 0·9 mm, and thecae generally 12 to 14 per cm, agreeing with the original description. Elles & Wood did not record the species from the Shelve area but its associates in the Rorrington Member match those at the type locality. A single specimen, Q.5331, from the Spy Wood Member, Loc. 369, may also belong here, as although it has a maximum width of only 0·6 mm it is in full relief in a fine sandstone.

A further specimen, Q.5329, from the Meadowtown Member, Loc. 314, is rather broader at 1·3 mm, and also appears to belong here, although as it has a very stout virgella it may be a different form.

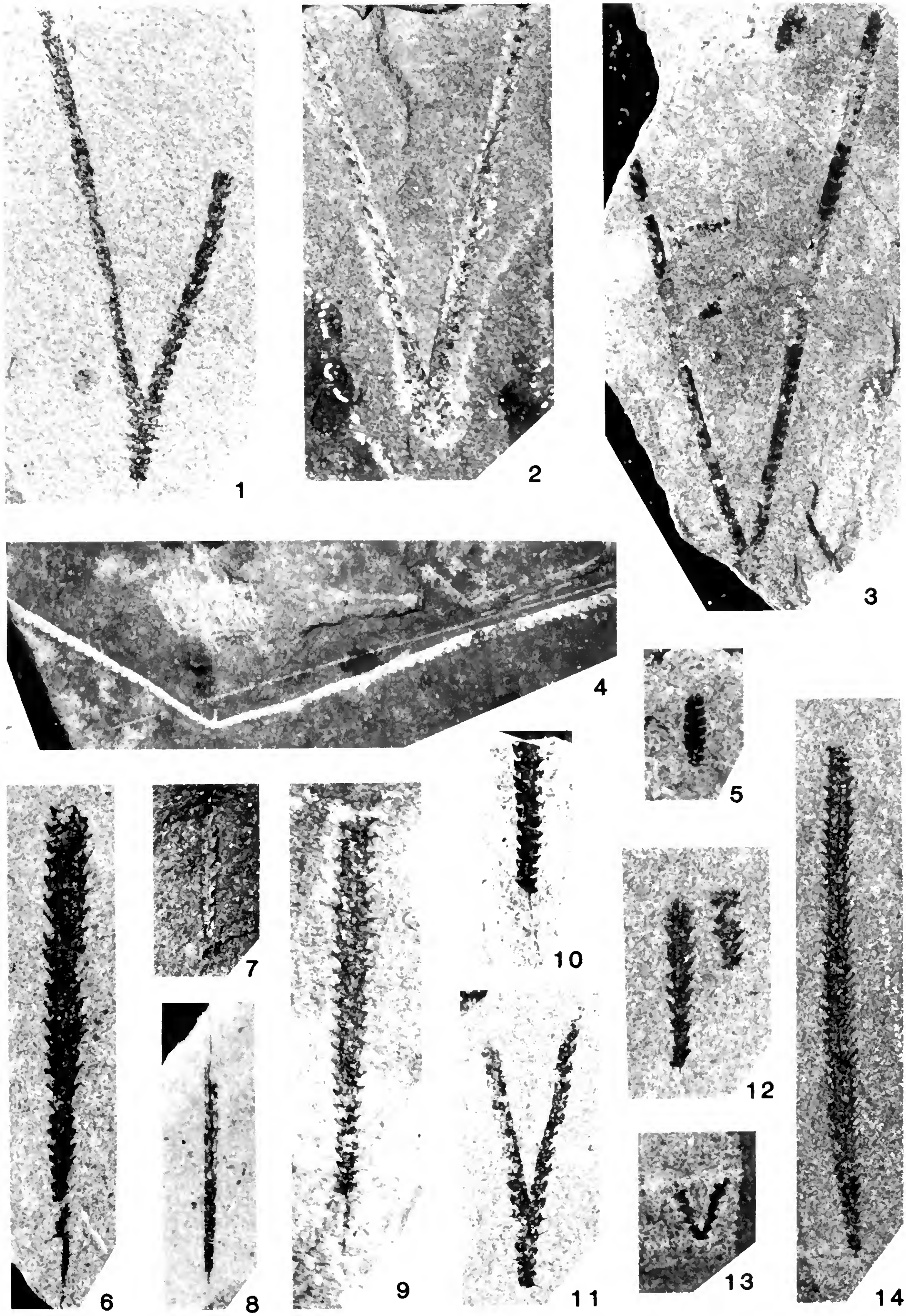
Climacograptus peltifer Lapworth 1876
Pl. 6, fig. 17

1876 *Climacograptus bicornis* var. *peltifer* Lapworth: pl. 2, fig. 53.
1906 *Climacograptus bicornis* var. *peltifer* Lapworth; Elles & Wood: 196; pl. 26, figs 10a–c.

DESCRIPTION. Rhabdosome 10 mm long, widening from 0·8 mm to 1·1 mm. Thecae 14 per cm with excavations occupying a third of the width of the rhabdosome and a quarter to a third of the free ventral wall. Proximal end with short stout virgella and long curved spines from the first two thecae, the spines then covered by a thin film extending up to the apertures of the second pair of thecae.

PLATE 5 Figs 1–7, 10 from Rorrington Member; Figs 8, 9, 11–14 from Spy Wood Member.

Fig. 1 *Dicranograptus rectus* Hopkinson, p. 32. Q.5289, Loc. 956. ×3. See also Text-fig. 28, p. 32.
Fig. 2 *Dicranograptus brevicaulis* Elles & Wood, p. 32. Q.5283, Loc. 374. ×3.
Fig. 3 *Dicranograptus rectus* Hopkinson, p. 33. Q.5290, Loc. 373. ×2.
Fig. 4 *Leptograptus latus* Elles & Wood, p. 29. **Lectotype** herein selected, GSM 49763, Spy Burn. ×2.
Fig. 5 *Pseudoclimacograptus modestus* (Ruedemann), p. 45. Q.5336, Loc. 334. ×3.
Fig. 6 *Orthograptus uplandicus* (Wiman), p. 40. Q.5320, Loc. 956. ×3.
Figs 7, 8 *Climacograptus brevis* Elles & Wood, above. Fig. 7, Q.5330, Loc. 519. Fig. 8, Q.5331, Loc. 369. Both ×3. See also Pl. 3.
Fig. 9 *Orthograptus uplandicus* (Wiman), p. 40. BU.2083 (Lapworth Collection), Beyrichia Bed, Rorrington. ×3. See also Text-fig. 34, p. 40.
Fig. 10 *Glyptograptus teretiusculus* (Hisinger), p. 38. Q.5309, Loc. 375. ×3. See also Text-fig. 32, p. 38.
Fig. 11 *Dicranograptus rectus* Hopkinson, p. 33. Q.5291, Loc. 417A. ×3.
Fig. 12 *Orthograptus uplandicus* (Wiman), p. 40. Q.5321, Loc. 333. ×3.
Fig. 13 *Dicellograptus exilis* Elles & Wood, p. 31. Q.5281, exact locality unknown. ×3.
Fig. 14 *Orthograptus* cf. *apiculatus* Elles & Wood, p. 39. Q.5311, Loc. 422. ×2.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Discussion. On the basis of identifications by Miss Elles, Whittard (1931) concluded that the fauna from Hagley Quarry indicated a level about the *clingani–linearis* Zones junction. Miss Elles listed this specimen (GSM RR2820) as *C. supernus* Elles & Wood, which would indicate an even higher level in the Ordovician. However, the specimen agrees well with the type of *C. peltifer* which is characteristic of a much lower horizon and the shelly fauna from the upper part of the Shelve succession fits more easily with the reassigned age when compared with other areas.

Climacograptus cf. ***tubularis*** Elles & Wood 1906
Pl. 6, fig. 2

cf. 1906 *Climacograptus Wilsoni* var. *tubularis* Elles & Wood: 199; pl. 26, fig. 13; text-fig. 129.

Rhabdosome 16 mm long, widening gradually from 0·9 mm to 1·3 mm, thecae 12 to 10 per cm, with excavations occupying one fifth of the width of the rhabdosome and a third of the free ventral wall. There is a stout virgella and the first pair of thecae have mesial spines. There is a straight median septum. The single specimen is in full relief, but much of the periderm has been lost owing to the coarse nature of the sediment. The general characters are those of *C. wilsoni* but there is no proximal sac developed. It is narrower than the specimens of *C. antiquus lineatus* and also has fewer thecae than that species as found in the Shelve area. The specimen, Q.5332, was found in the Aldress Member, Loc. 304.

Climacograptus sp.
Fig. 35; Pl. 6, fig. 9

A single specimen, Q.5333, from the Aldress Member, Loc. 344, has a well-developed proximal spine and was at first considered to be *C. spiniferus* Ruedemann. Close examination, however, shows that the spine is either a very stout sicular apertural spine (not usually seen in this type of *Climacograptus*) or a genicular spine from $th1^2$. The rock is broken away from much of the proximal end but there seems to be little trace of a corresponding spine on $th1^1$. However, a stout virgella may have been present. The rhabdosome is about 4 mm long and reaches a width of 1·1 mm. There are 5 thecae in 3·5 mm. In general size the specimen approaches *C. pygmaeus* Ruedemann (1925) but is clearly not a *typicalis* type as the sicula is not exposed below $th1^2$. *C. prolificus* Parks (1928) is also described as having two 'apertural spines' but Riva (1974) regards it as a synonym of *C. pygmaeus. C. praesupernus* Obut & Sobolevskaya 1964 has three spines at the proximal end, the lateral ones being about 1 mm long. This is rather stouter than the single spine preserved on this specimen but the other dimensions match fairly well. Tzaj's further account (1976) of this Russian species does not add any more detail or clear figures to help in identification. As only the single example is so far known from Shelve, it is best left without formal identification.

Fig. 35 *Climacograptus* sp. Q.5333, Loc. 344. Enlargement of Pl. 6, fig. 9, × 10.

Genus ***PSEUDOCLIMACOGRAPTUS*** Přibyl, 1947

TYPE SPECIES. *Climacograptus Scharenbergi* Lapworth 1876.

Pseudoclimacograptus scharenbergi (Lapworth 1876)
Pl. 6, figs 12, 18

1876 *Climacograptus Scharenbergi* Lapworth: pl. 2, fig. 55.
1906 *Climacograptus Scharenbergi* Lapworth; Elles & Wood: 206; pl. 27, figs 14a–e; text-figs 139a–c.

DISCUSSION. This species is fairly common in the Hagley and Whittery Members but does not seem to occur lower. The preservation, although often in relief, is not generally good as the specimens are distorted. Distinction from *P. modestus* is mainly on thecal count (*modestus* with 9 thecae in first 5 mm, *scharenbergi* with 7) and as noted by Bulman (1948) the proximal end in *scharenbergi* tapers rather more than in *modestus*. The development of the virgella and proximal thecal spines is very variable. A few specimens appear to show supragenicular walls slightly inclined inwards as in *C. s. angulatus* Bulman, but they lack the steeply inclined apertures of that form.

MATERIAL AND HORIZONS. Hagley Member: Q.5334, Loc. 399; Q.5335, Loc. 392A. Whittery Member: Q.5345, Loc. 272.

Pseudoclimacograptus modestus (Ruedemann 1908)
Pl. 5, fig. 5

1908 *Climacograptus modestus* Ruedemann: 432; pl. 28, fig. 30; text-figs 400–403.

This species is not very common in the collection but has been found in the Rorrington Member, Q.5336, Loc. 334, and similar forms with a high thecal count occur in the Whittery Member, Q.5359, Loc. 272. There seems to be some distortion in many of the specimens. A critical revision of the species is required since Ruedemann's (1908) account is quite inadequate and Riva (1974) did not figure or discuss the type material. The type of *C. parvus* Hall (figured by Riva, 1974) appears to be closer to *modestus* than to *scharenbergi*, assuming that Riva is correct in assigning it to *Pseudoclimacograptus*.

Family **LASIOGRAPTIDAE** Lapworth, 1879

Genus ***LASIOGRAPTUS*** Lapworth, 1873

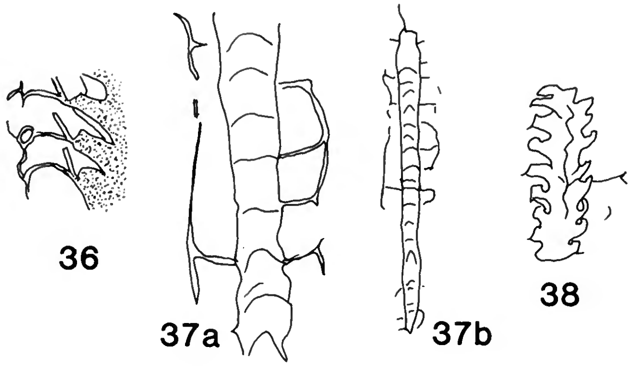
TYPE SPECIES. *Lasiograptus costatus* Lapworth 1873.

Lasiograptus costatus Lapworth 1873
Figs 36–38; Pl. 6, figs 5, 8

1873 *Lasiograptus costatus* Lapworth: 559.
1908 *Lasiograptus* (*Thysanograptus*) *Harknessi* var. *costatus* (Lapworth); Elles & Wood: 327; pl. 34, figs 2a–d; text-figs 215a–g.

DESCRIPTION. Rhabdosome small, rarely more than 1 cm long, widening from 1·2 mm to 2·0 mm, exclusive of lacinia. Thecae 16 per cm, of characteristic lasiograptid type, excavations sloping inwards and occupying about a third of the width of the rhabdosome, supragenicular wall inclined at about 45°, genicular spines stout, slightly curved, up to 1 mm long, occasionally seen to form a lacinia.

DISCUSSION. The above description is based on the Shelve specimens, some of which are well preserved in partial relief. They do not show the well-developed ventral lacinia seen in many of the original Scottish specimens, including the type, but this is probably the result of different preservation. In the black shales the specimens are reduced to a virtually flat silvery film and the three-dimensional nature of the lacinia is not so clear. The type specimen, however, shows that the single apertural process divides laterally almost at once and each branch grows out for



Figs 36–38 *Lasiograptus costatus* Lapworth. Fig. 36, BU.1341, Hartfell Shales, Dobb's Linn. Part of lectotype (sel. Elles & Wood 1908: pl. 34, fig. 2b) showing lateral bifurcation of apertural spine and subsequent development of the lacinia, ×7. Fig. 37a, b, on same slab as Sedgwick Museum, Cambridge, SM A23399, scalariform view. a, ×7; b, ×2½. Fig. 38, Q.5337, Loc. 343A. Drawing of Pl. 6, fig. 8, ×5.

about 1 mm before dividing again in the vertical direction, the divisions then joining up with those from the thecae above and below to form vertical rods which in a few cases show traces of lateral connections. This structure was described by Elles & Wood (1908), but its full three-dimensional nature does not seem to have been realised. Their figure of a 'scalariform view' (Elles & Wood 1908: text-fig. 215e) is in fact only subscalariform and like most views shows effectively only a single strand on each side. On the same slab as another of their figured specimens is a fine true scalariform view (Fig. 37) showing also a single vertical lacinial thread on each side. The specimen is in a blocky mudstone and excavation, if possible, might reveal the other parts of the lacinia. What it suggests is that the cross section of the total rhabdosome is approximately square with the vertical strands at the corners, although the thecal part is more or less rectangular with its width being about twice the thickness.

The species has been described from Kazakhstan by Tzaj (1976), but his specimens have much longer thecal spines with no trace of vertical lacinia and they are probably a different form. Geh (1963) has also figured specimens from China as this species, but his text-figure shows the characters of *L. spinatus* Hadding which has a more tapering rhabdosome. *Paraclimacograptus weberi* Keller 1956, although incomplete, looks very close to some of the Shelve specimens.

Material and horizon. The species occurs in a few localities of the Aldress Member, including the *Dictyonema* horizon: Q.5337, Loc. 343A; Q.5349, Loc. 344; Q.5350, Loc. 346.

Genus *GYMNOGRAPTUS* Bulman 1953

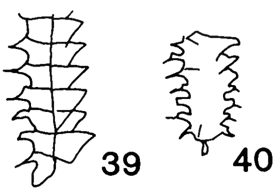
Type species. *Diplograptus linnarssoni* Moberg 1896.

There seems to be some difficulty in the identification of this genus in spite of the detailed studies of isolated material (Urbanek 1959, Jaanusson 1960). The earliest illustrations of the type species *Diplograptus linnarssoni* by Moberg (1896) show thecae which are denticulate at most, and the first full description by Hadding (1913) mentions thecal 'denticles', the figures showing no trace of spines. Bulman's (1953) account giving the first description of the genus says 'thecae . . . provided with long apertural spines.' Certainly the topotypic material in the Lapworth Collection in Birmingham (labelled '*Gymnograptus Linnarssoni* Tullb. mscr. Fågelsång. 1878. S. A. Tullberg.') shows long spines on the thecae in flattened material but a speci-

men in relief does not show any spines, agreeing with Hadding's illustration of a relief specimen. Wang (1978) has proposed a second species, *G. spinatus*, on the assumption that *G. linnarssoni* does not have spines. Both forms have a zigzag median suture although it is not so well seen in *G. spinatus*. This suggests that the two forms may simply represent preservational differences. Lee (1963) noted thecal spines on his material and his illustrations show some thecae approaching the lasiograptid condition, particularly proximally. Urbanek (1959) pointed out that his fragmentary *Gymnograptus* sp. was very similar to the type of *Lasiograptus retusus* Lapworth which has a somewhat zigzag median septum. *L. retusus*, however, has its own problems as it is based on a single specimen showing no spines. The spined forms attributed to it by Elles & Wood (1908: pl. 34, figs 3b, c) are not conspecific with the holotype (1908: pl. 34, fig. 3a), as has been recognized by later workers. Lee (1963) made *L. retusus* the type of his new genus *Prolasiograptus*, but his Chinese specimen is much wider than the type of *retusus* and his new species *P. asiaticus* is nearer. Both forms, however, show the small first theca which is a feature of *Gymnograptus* (Lee 1963: text-figs 6 and 7c). The proximal end in the type specimen of *retusus* is not clear enough to show whether or not it has this feature.

Gymnograptus (?) sp.
Figs 39, 40; Pl. 3, figs 10, 15, 16

DESCRIPTION. Rhabdosome up to 3 cm long, widening from about 1·0–1·2 mm at the proximal end to 2·0 mm in the first 10 mm and slowly afterwards to a maximum of 3·0 mm. Thecae 8 to 10 in the first 5 mm but only 7 in 5 mm distally, of gymnograptid type with a short supragenicular wall inclined inwards in the distal thecae and bearing stout genicular spines up to 1 mm long. Proximal end not well preserved but more or less rounded and with prominent virgella.



Figs 39, 40 *Gymnograptus* (?) sp. Fig. 39, Q.5338, Loc. 234. Enlargement of part of Pl. 3, fig. 10. Fig. 40, BU.2082, Betton Dingle. Proximal end of Pl. 3, fig. 16. Both ×5.

DISCUSSION. This form is fairly common in the Betton Member but is poorly preserved. It agrees fairly well with one of the specimens figured by Elles & Wood as *Lasiograptus retusus*, but not with the holotype of that species which shows a fairly strong zigzag septum and no trace of thecal spines. The shape of the thecae is strongly reminiscent of *Gymnograptus linnarssoni*, but the proximal end is rounded and there is a stout virgella. Some of the specimens show distinct grooves at right angles to the median septal line which are similar to those figured by Berry (1964) in his Norwegian *Amplexograptus munimentus* and *A. tubulus*. Both species are from the same horizon as the Shelve specimens, but Berry makes no mention of thecal spines and his forms have slightly fewer thecae per cm. However, in view of the difficulty noted earlier in seeing spines in some preservations of *Gymnograptus*, it is possible that the Norwegian species are actually gymnograptids.

Since the Shelve specimens are not well preserved, it has been felt better to leave them under an open nomenclature until the other problems are cleared up. The association with pendent didymograptids in the Betton Member is earlier than the standard range of *Gymnograptus* in Scandinavia and China where it always occurs immediately post-*murchisoni* Zone.

MATERIAL AND HORIZON. Betton Member: Q.5338, Loc. 234; Q.5339–40, Loc. 388; Q.5341–2, Loc. 232.

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Appendix: Locality list

Most of the localities have been traced on Whittard's field maps although some are still doubtful. The species listed include some that have not been checked by critical re-examination of specimens but are added to indicate the range of species present at each locality.

54. 975 m at 358° from Hope Hall, Hope. SJ 3482 0290. Hope Member. *Didymograptus pluto*; *Acrograptus acutidens*; *A. gracilis*; ? *Glyptograptus dentatus.*
58. Stream section 716 m at 126° from Bench Mark 122 m by road at Leigh Hall. SJ 3399 0312. Hope Member. *Acrograptus gracilis.*
132. 881 m at 91° from Methodist Chapel, Meadowtown. SJ 3201 0120. Stapeley Shale Member. *Glossograptus* cf. *acanthus*; *Acrograptus* cf. *acutidens.*
133. same as 132. *Didymograptus pluto*; *D.* cf. *stabilis*; *Glossograptus fimbriatus*; ? *Triarthrus* sp.
140. 1868 m at 293° from Stiperstones Inn. SJ 3464 0116. Hope Member. *Didymograptus* cf. *stabilis.*
144. Section with centre 533 m at 242° from Methodist Chapel, Meadowtown. SJ 3065 0097. Meadowtown Member. *Dicellograptus* cf. *sextans*; *Dicranograptus irregularis.*
164. 158 m at 260° from Methodist Chapel, Meadowtown. SJ 3096 0120. Meadowtown Member. *Dicellograptus divaricatus*; *D.* cf. *sextans*; cf. *Cryptograptus* sp.; cf. *Dictyonema* sp.
169. Stream section 646 m at 25° from NE corner of Hogstow Hall, west of Crowsnest. SJ 3677 0178. Hope Member. *Didymograptus pluto*; *Expansograptus* cf. *euodus.*
204. Section centred on 1268 m at 316° from Hope Church. SJ 3322 0242. Hope Member. *Didymograptus pluto*; ? hyolithid.
222A. 600 m W of Leigh Manor, on edge of Overton's Wood. SJ 3311 0229. Hope Member. *Didymograptus pluto.*
232. 661 m at 50° from Methodist Chapel, Meadowtown. SJ 3164 0164. Betton Member. *Didymograptus murchisoni*; ? *Gymnograptus* sp.
234. In Betton Dingle, 230 m NW of Lyde Cottage. SJ 3165 0169. Betton Member. *Didymograptus murchisoni*; *Gymnograptus*? sp.
272. Stream section 250 m south of Chirbury. SO 2620 9810. Whittery Member. *Orthograptus truncatus*; *Pseudoclimacograptus scharenbergi*; *P.* cf. *modestus.*
279. 300 m ENE of The Bog. SO 3595 9789. Mytton Member. ? *Tetragraptus* sp.
294. Spring Coppice, 866 m at 167° from Bench Mark 359·5 (ft) beside Woodmore, near Wotherton. Whittery Member. SO 2783 9960. *Diplograptus foliaceus*; *Dictyonema* sp.
299. Old quarry in Whittery Wood, 1768 m at 290° from Methodist Chapel, Priestweston. SO 2747 9808. Whittery Member. *Diplograptus foliaceus*; *Amplexograptus* cf. *fallax*; *Orthograptus calcaratus vulgatus.*
302. Stream section 800 m east of Wotherton, at point 1963 m at 174° from St Mark's Church, Marton. SJ 2905 0066. Aldress Member. *Diplograptus leptotheca*; *Orthograptus truncatus*; *Climacograptus* cf. *antiquus*; *Dictyonema fluitans.*
304. West of same stream, 1628 m at 174° from St Mark's Church, Marton. SJ 2902 0068. Aldress Member. *Diplograptus leptotheca*; *Orthograptus* cf. *uplandicus*; *Climacograptus* aff. *antiquus lineatus*; *C.* cf. *tubularis.*
307. 302 m WSW of Little Weston. SO 2903 9832. Betton Member. *Didymograptus* cf. *stabilis*; *D.* cf. *murchisoni.*
314. Laneside exposure 360 m W of Little Weston. SO 2894 9856. Meadowtown Member. *Dicranograptus* sp.; *Climacograptus* cf. *brevis.*
318. In Ox Wood, 450 m NW of Rorrington Lodge. SJ 2905 0082. Aldress Member. *Amplexograptus fallax.*
324. Old quarry 400 m NW of Little Weston. SO 2910 9878. Meadowtown Member. *Dicellograptus sextans*; *Dicranograptus irregularis*; *Climacograptus* sp.
329. Road section 1950 m at 10° from Methodist Chapel, Priestweston. SO 2950 9935. Meadowtown Member. *Cryptograptus schaeferi*; *Glyptograptus* sp.
333. Trackside exposure 500 m SW of Rorrington. SJ 2965 0027. Spy Wood Member. *Orthograptus* cf. *apiculatus*; *O. uplandicus.*

334. Grey Grass Dingle, 2164 m at 306° from Stapeley Farmhouse. SJ 2977 0017. Rorrington Member. *Nemagraptus gracilis*; *Leptograptus* cf. *validus*; *Dicranograptus brevicaulis*; *Diplograptus leptotheca*; *Pseudoclimacograptus modestus*.

343A. 1689 m at 337° from Methodist Chapel, Old Church Stoke. SO 2830 9640. Aldress Member. *Cryptograptus tricornis*; *Diplograptus multidens*; *Orthograptus* cf. *apiculatus*; *Climacograptus* cf. *brevis*; *Lasiograptus costatus*.

344. Aldress Dingle, 1454 m at 330° from Methodist Chapel, Old Church Stoke. SO 2788 9601. Aldress Member. *Diplograptus* cf. *leptotheca*; *Orthograptus* sp.; *Climacograptus* sp.; *Lasiograptus* cf. *costatus*; *Dictyonema fluitans*.

346. 2252 m at 348° from Methodist Chapel, Old Church Stoke. SO 2821 9705. Aldress Member. *Cryptograptus* sp.; *Diplograptus* sp; *Amplexograptus fallax*; *Lasiograptus* cf. *costatus*.

352. 2243 m at 353° from Methodist Chapel, Old Church Stoke. SO 2841 9707. Rorrington Member. *Nemagraptus* sp.; *Leptograptus validus*; ? *Dictyonema* sp.

355. 1923 m at 342° from Methodist Chapel, Old Church Stoke. SO 2811 9684. Aldress Member. *Cryptograptus tricornis*; *Corynoides* cf. *curtus*; *Diplograptus* cf. *leptotheca*; *Orthograptus* sp.; *Climacograptus* cf. *brevis*.

369. 1091 m at 333° from Methodist Chapel, Old Church Stoke. SO 2816 9582. Spy Wood Member. *Orthograptus* cf. *uplandicus*; *Climacograptus brevis*.

371. River bank in Spy Wood, 90 m NE of Spy Wood Cottage. SO 2820 9579. Rorrington Member. *Nemagraptus gracilis*; *Leptograptus validus*; *Dicranograptus brevicaulis*.

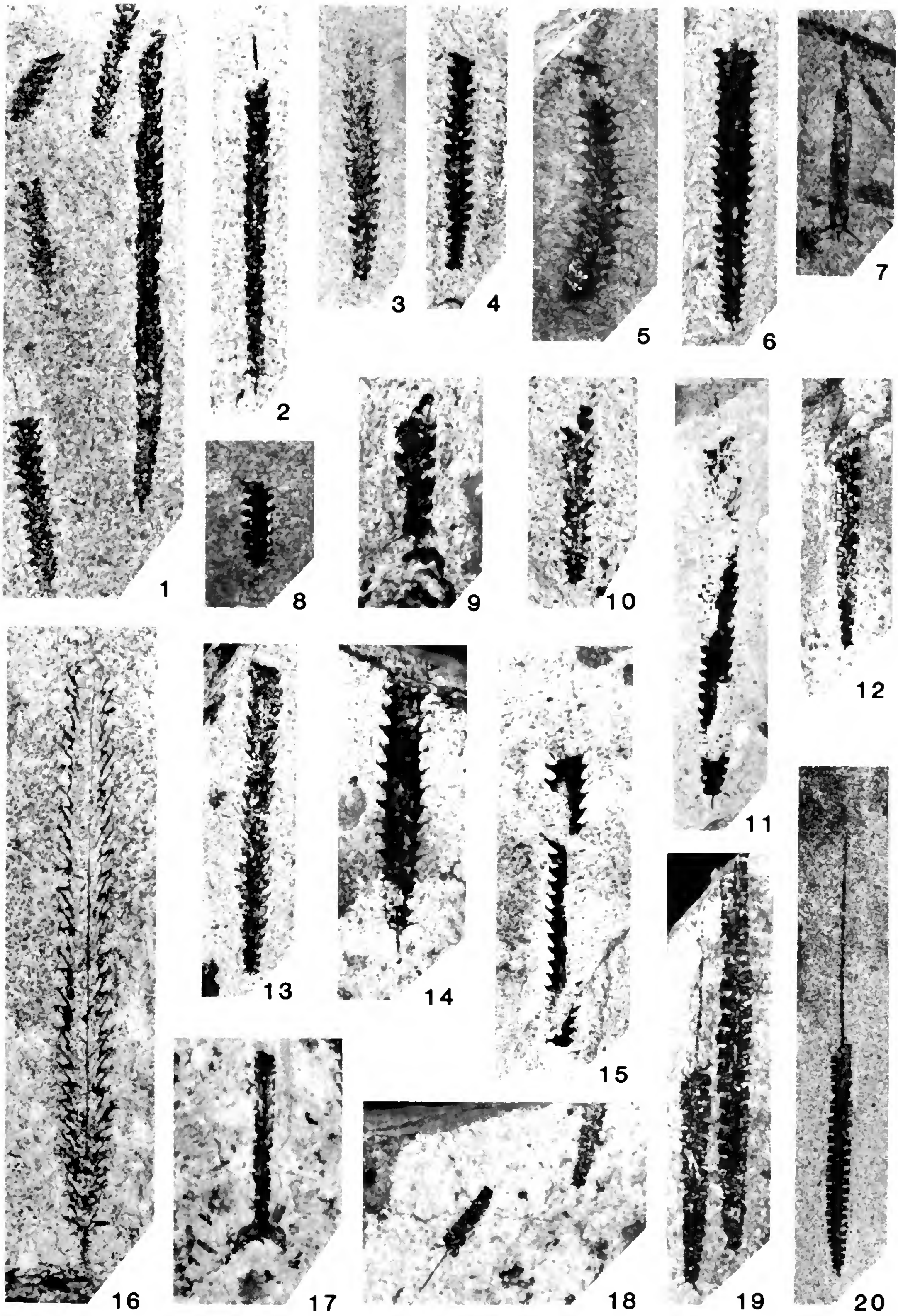
373. 1070 m at 334° from Methodist Chapel, Old Church Stoke. SO 2821 9580. Rorrington Member. *Leptograptus validus*; *Dicranograptus rectus*; *Amplexograptus* sp.; *Orthograptus* sp.; *Pseudoclimacograptus modestus*; *Dictyonema* sp.

374. 1082 m at 335° from Methodist Chapel, Old Church Stoke. SO 2823 9583. Rorrington Member. *Leptograptus validus*; *Dicellograptus* cf. *intortus*; *Dicranograptus brevicaulis*; *Pseudoclimacograptus* cf. *modestus*.

375. Aldress Dingle, 1079 m at 336° from Methodist Chapel, Old Church Stoke. SO 2823 9584. Rorrington Member. *Leptograptus* cf. *validus*; *Dicellograptus* sp.; *Glyptograptus teretiusculus*; *Pseudoclimacograptus* cf. *modestus*.

PLATE 6 Figs 1–9 from the Aldress Member; Figs 10, 11, 14, 15 from the Whittery Member and Figs 12, 13, 16–20 from the Hagley Member.

Fig. 1 *Climacograptus* aff. *antiquus lineatus* Elles & Wood, p. 41 (long specimen on right). Q.5326. Also *Diplograptus leptotheca* Bulman, p. 36. Q.5297, Loc. 304. ×3.
Fig. 2 *Climacograptus* cf. *tubularis* Elles & Wood, p. 44. Q.5332, Loc. 304. ×3.
Figs 3, 4 *Diplograptus leptotheca* Bulman, p. 36. Fig. 3, Q.5298; Fig. 4, Q.5299a; both Loc. 302. Both ×3.
Fig. 5 *Lasiograptus costatus* Lapworth, p. 45. BU.2084, Lower Point, Aldress Burn. ×3.
Fig. 6 *Orthograptus truncatus* Lapworth, p. 40. Q.5316, Loc. 302. ×3.
Fig. 7 *Cryptograptus tricornis* (Carruthers), p. 25. Q.5257, Loc. 343A. ×3.
Fig. 8 *Lasiograptus costatus* Lapworth, p. 45. Q.5337, Loc. 343A. ×3. See also Text-fig. 38, p. 46.
Fig. 9 *Climacograptus* sp., p. 44. Q.5333, Loc. 344. ×6. See also Text-fig. 35, p. 44.
Figs 10, 11 *Diplograptus foliaceus* (Murchison), p. 34. Fig. 10, Q.5295, Loc. 747. Fig. 11, Q.5296, Loc. 294. Both ×3. See also Pl. 3.
Fig. 12 *Pseudoclimacograptus scharenbergi* (Lapworth), p. 45. Q.5334, Loc. 399. ×3.
Fig. 13 *Diplograptus leptotheca* Bulman, p. 36. Q.5300, Loc. 744. ×3.
Fig. 14 *Orthograptus calcaratus vulgatus* Elles & Wood, p. 40. Q.5314, Loc. 299. ×3.
Fig. 15 *Orthograptus truncatus* Lapworth, p. 40. Q.5318, Loc. 272. ×3.
Fig. 16 *Orthograptus calcaratus vulgatus* Elles & Wood, p. 40. Q.5315, Loc. 739. ×3.
Fig. 17 *Climacograptus peltifer* Lapworth, p. 42. GSM RR2820, Hagley Quarry. ×3.
Fig. 18 *Pseudoclimacograptus scharenbergi* (Lapworth), p. 45. Q.5335, Loc. 392A. ×3.
Figs 19, 20 *Climacograptus* aff. *antiquus lineatus* Elles & Wood, p. 41. Fig. 19, Q.5327, Loc. 392A. ×3. Fig. 20, Q.5328, Loc. 744. ×2. See also Pl. 3.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377. 1170 m at 342° from Methodist Chapel, Old Church Stoke. SO 2830 9596. Rorrington Member. *Dicellograptus sextans*; *Nemagraptus gracilis*; *Ptilograptus* sp.
382A. 1347 m at 357° from Methodist Chapel, Old Church Stoke. SO 2858 9618. Betton Member. *Didymograptus murchisoni*.
388. 1146 m at 349° from Methodist Chapel, Old Church Stoke. SO 2847 9596. Betton Member. *Didymograptus murchisoni*; *Gymnograptus*? sp.
389. 1161 m at 347° from Methodist Chapel, Old Church Stoke. SO 2841 9596. Rorrington Member. *Dicellograptus intortus*.
390. 1170 m at 345° from Methodist Chapel, Old Church Stoke. SO 2836 9597. Rorrington Member. *Nemagraptus gracilis*; *Dicellograptus* cf. *divaricatus*; *D. intortus*; *Climacograptus brevis*; *Pseudoclimacograptus* sp.; ? *Acanthograptus* sp.
392A. River bank in Spy Wood, 160 m N of Rock House. SJ 2762 9578. Hagley Member. *Climacograptus* aff. *antiquus lineatus*; *Pseudoclimacograptus scharenbergi*.
394. Brynkin Dingle, 100 m NW of Bryncyn Green. SO 2805 9555. Spy Wood Member. *Dicellograptus intortus*; *Climacograptus* cf. *brevis*; *Orthograptus* cf. *uplandicus*.
395. Brynkin Dingle, 190 m NW of Bryncyn Green. SO 2801 9563. Aldress Member. *Orthograptus* cf. *apiculatus*; *Cryptograptus tricornis*; *Dictyonema fluitans*.
399. Old quarry 200 m N of Church Stoke Hall, SJ 2746 9419. Hagley Member. *Pseudoclimacograptus scharenbergi*.
413. Lane 91 m SW of Rorrington Hall. SJ 2982 0065. Spy Wood Member. *Orthograptus* cf. *uplandicus*.
417A. Track 90 m due E of Rorrington Hall. SJ 2995 0074. Spy Wood Member. *Dicellograptus* sp.; *Dicranograptus rectus*; *Orthograptus* sp.
422. 365 m SW of Lower Wood Farm. SJ 3062 0232. Spy Wood Member. *Orthograptus* cf. *apiculatus*; *O.* cf. *uplandicus*.
437. Section along Holywell Brook, 440 m SE of Rorrington. SJ 3036 0027. Betton Member. *Didymograptus murchisoni*.
444. 1231 m at 301° from Stapeley Farmhouse, near Whitegrit. SO 3044 9950. Weston Member. *Didymograptus murchisoni*.
463. Long section extending from point 1268 m at 334° to another point 1256 m at 349°, both measured from Stapeley Farmhouse. SJ 3097 0000 to 3128 0009. Stapeley Member. *Didymograptus* aff. *miserabilis*.
479. Stream section 400 m S of Desert. SJ 3059 0148. Rorrington Member. *Dicellograptus* cf. *sextans*; *D. salopiensis*; *Dicranograptus brevicaulis*.
493. Stream section 90 m N of Desert. SJ 3066 0198. Rorrington Member. *Nemagraptus gracilis* cf. *distans*; *Dicellograptus exilis*.
497. Lower Wood Farm. SJ 3085 0260. Rorrington Member. ? *Nemagraptus* sp.; *Dicellograptus sextans*; *D. divaricatus*.
503. 573 m at 220° from Methodist Chapel, Meadowtown. SJ 3074 0080. Meadowtown. Member. *Cryptograptus schaeferi*; *Dicellograptus* cf. *vagus*; *Dicranograptus* cf. *irregularis*.
519. 546 m at 324° from Methodist Chapel, Meadowtown. SJ 3080 0168. Rorrington Member. cf. *Nemagraptus* sp.; cf. *Leptograptus* sp.; *Climacograptus brevis*.
536. 1247 m at 31° from Methodist Chapel, Meadowtown. SJ 3180 0225. Betton Member. *Didymograptus murchisoni*; *D.* aff. *miserabilis*; ?*Gymnograptus* sp.; lingulid.
563. 168 m at 33° from Methodist Chapel, Meadowtown. SJ 3120 0138. Meadowtown Member. *Diplograptus* cf. *foliaceus*.
575A. 300 m at 177° from Methodist Chapel, Meadowtown. SJ 3116 0092. Betton Member. *Diplograptus* cf. *foliaceus*.
594. Grey Grass Dingle, 500 m due S of Rorrington Hall. SJ 2988 0028. Rorrington Member. *Nemagraptus gracilis*; *Leptograptus* sp.
635. Farmyard at Brithdir Farm. SO 3010 9528. Hope Member. *Pseudophyllograptus* cf. *angustifolius*; *Didymograptus pluto*; *D.* cf. *stabilis*.
701. East side of Ritton Castle. SO 3452 9772. Hope Member. *Acrograptus acutidens*; *Glyptograptus dentatus*.
720. Road section beside All Saints Church, Shelve, plus adjacent field exposures. SO 3365 9901. Mytton Member (Shelve Church Beds). *Corymbograptus deflexus*; *C.* cf. *inflexus*; *Expansograptus* cf. *nitidus*; *E.* cf. *sparsus*; *Glyptograptus shelvensis*.
739. 158 m at 329° from St Michael's Church, Church Stoke. SO 2705 9413. Hagley Member. *Orthograptus calcaratus vulgatus*; *Diplograptus* cf. *foliaceus*; *Climacograptus* sp.
744. 1271 m at 287° from Methodist Chapel, Old Church Stoke. SO 2745 9525. Hagley Member. *Diplograptus leptotheca*; *Climacograptus* aff. *antiquus lineatus*.

747. Old quarry 465 m NW of Rock House. SO 2740 9603. Whittery Member. *Diplograptus foliaceus*; *Dictyonema* sp.
779. Laneside exposure 100 m S of Tankerville Mine. SO 3555 9937. Mytton Member. *Tetragraptus* cf. *bigsbyi*; didymograptid.
783. Bergam Quarry, 567 m at 5° from Methodist Chapel, Pennerley. SO 3565 9976. Mytton Member (Tankerville Flags). *Expansograptus* cf. *nitidus*; *E.* cf. *praenuntius*; *E.* cf. *suecicus*.
791. Tip heaps 120 m east of Tankerville Mine. SO 3664 9946. Mytton Member. *Isograptus* sp.
834. Road section 472 m at 110° from Hope Church. SJ 3455 0133. Hope Member. *Didymograptus pluto*.
834N. 360 m SW of Hope Rectory. SJ 3388 0125. Hope Member. *Acrograptus* cf. *acutidens*.
853A. 664 m at 69° from Stiperstones Inn. SJ 3692 0070. Mytton Member. *Expansograptus* cf. *simulans*.
905. 1268 m at 9° from All Saints Church, Shelve. SJ 3392 0025. Mytton Member. *Expansograptus* cf. *nitidus*; *E.* cf. *simulans*; *Glyptograptus dentatus*; various dendroids.
922. Hope Valley (Shropshire Sheet 47/12), not localized. Hope Member. *Pseudophyllograptus* (?) cf. *glossograptoides*.
933. 1128 m at 357° from All Saints Church, Shelve. East Roman Gravels. SJ 3348 0032. Mytton Member (Tankerville Flags). *Clonograptus* sp.; dichograptid stipes; dendroids.
946. Shale exposed in water pipeline leading to digging, north end of Todleth Hill. SO 290 950. Stapeley Member. *Amplexograptus* cf. *confertus*.
956. 1369 m at 245° from Methodist Chapel, Meadowtown. SJ 2990 0066. Rorrington Member, passage beds to Spy Wood Member. *Nemagraptus gracilis*; *Dicellograptus* cf. *exilis*; *Dicranograptus brevicaulis*; *D. rectus*; *Orthograptus uplandicus*.
957A. 200 m NE of Betton Wood Farm. SJ 3134 0255. Meadowtown Member. *Climacograptus* aff. *antiquus lineatus*.
959. In wood, 650 m SE of Lyde. SJ 3205 0106. Hope Member. *Didymograptus pluto*; *Amplexograptus* cf. *confertus*; *Glyptograptus* sp.

Lyde Stream junction. SJ 3180 0149. Weston Member. *Didymograptus murchisoni*.

Illing Collection of Hope Member. No locality. *Glossograptus* cf. *armatus*; *Climacograptus* cf. *angustatus*; *Didymograptus* cf. *stabilis*; *Acrograptus* cf. *acutidens*.

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Accepted for publication 10 September 1984

British Museum (Natural History)

An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

Bulletin of the British Museum (Natural History), Geology series
Vol. 33 No. 1. Dec. 1979. 69pp. 38 figs. Large full-colour map

The late Professor W. F. Whittard, F.R.S., who died in 1966, devoted much of his life to the study of the Shelve Inlier, and his great monograph on its trilobites remains fundamental. The area, in west Salop (including a small part of north Powys), was the scene of famous early geological studies by Murchison and Lapworth. By Palaeozoic standards it is in places richly fossiliferous, and exhibits the best continuous Ordovician succession in Britain, one which is indeed almost complete. This classic area is of continuing interest, not only to professionals but also to amateur geologists and students, few of whom complete their studies without at least one field visit; but amazingly this is the first detailed map ever to be published. That the work of Whittard, now made available through the efforts of Professor W. T. Dean of Cardiff, is authoritative there can be no doubt: for over thirty-five years he studied these rocks, unravelling their complexities and perfecting his map.

The work complete with map, £10.50 (Post & packing 30p)
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By A. Williams

Bull. B.M. (N.H.), Geology Supplement 11, 1975. 163pp., 28 plates, 5 tables, 11 text figs. £13.00 (P & p. 50p)

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The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae

D. N. Lewis

Geology series Vol 40 No 2 29 May 1986

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The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae

D. N. Lewis

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis

Boletechinus delawaricus sp. nov. from the Upper Cretaceous of Delaware, U.S.A. and *B. rowei* (Gregory) *anglicus* subsp. nov. from the Upper Cretaceous of England are described for the first time, and *Zeuglopleurus costulatus* Gregory, *Boletechinus rowei rowei* (Gregory) and *B. mcglameryae* Cooke are redescribed. The new family Zeuglopleuridae is erected to comprise *Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*. *Zeuglopleurus rowei* Gregory from the English Upper Cretaceous is referred to the genus *Boletechinus*, and one of the original syntypes of *Z. rowei* is made the holotype of the new subspecies *B. rowei anglicus*.

Introduction

The 'regular' echinoid *Boletechinus* has until now been recorded only from the Maastrichtian of Sumter County, Alabama where it is represented by one species, *B. mcglameryae*, described by C. Wythe Cooke in 1955. It was therefore interesting to receive from Mr R. Baker of Ramsgate, Kent, three specimens of *Boletechinus* from the Navesink Marl of the Delaware Canal, Delaware.

This paper describes the new species of *Boletechinus* from the Maastrichtian, Navesink Marl of Delaware, examines the English species of *Zeuglopleurus* and *Boletechinus*, and discusses their classification with respect to the Glyphocyphidae and the Temnopleuridae.

Relatively few echinoids have been described from the Upper Cretaceous of Delaware, whereas other types of fossil are well represented. C. Wythe Cooke (1958) opened his work by stating '... On the following pages are described all the echinoids known from the Upper Cretaceous deposits of the Atlantic Coastal Plain north of Virginia ...' and described twelve

species, of which only four 'irregular' echinoids are from Delaware. Of these four, *Faujasia geometrica* (Morton) and *Hardouinia florealis* (Morton) are probably from the Marshalltown Formation (Campanian). *Hemiaster delawarensis* Clark is probably from the Mount Laurel Sands (Campanian), while *H. ungula* Morton comes from an unknown formation. None of them are from the Navesink Marl of Delaware, but *Oolopygus williamsi* Clark comes from the Navesink Marl of New Jersey. Clark (1915) did not describe any 'regular' urchins from Delaware, but listed ?*Pygurus geometricus* (Morton) and *Cassidulus florealis* (Morton) from the Matawan Formation (Campanian). 'Regular' echinoids from the Upper Cretaceous of Delaware or nearby locations were not recorded by either author.

In the classification used in the *Treatise* (Fell 1966: U408) the genus *Boletechinus* was placed under the heading 'Family Uncertain'. With the addition of other species of *Boletechinus* it becomes clear that the genus shares a number of characters in common with *Zeuglopleurus*, until now regarded as a member of the family Temnopleuridae. In both genera the ocular plates I and V are insert and the compounding of the ambulacral plates follows the acrosaleniid pattern (*sensu* Jensen 1981: 50–55; see Fig. 1.)

In redescribing the American type species of *Boletechinus* and describing the new American species for the first time, it became apparent that close comparison with *Zeuglopleurus* was necessary.

In 1889 Gregory described *Zeuglopleurus costulatus* using specimens E4365, 75556a and 75556b. He regarded 75556a and 75556b as juveniles of the species, but selected no type. In 1900, Gregory described *Z. rowei* using E39372, and also 75556a and 75556b which he no longer regarded as juveniles of *Z. costulatus*. Again, he did not select a type. In the present paper, *Z. rowei* is transferred to the genus *Boletechinus* and *B. rowei* is divided into two subspecies—*B. rowei rowei* and *B. rowei anglicus*. The lectotype of *B. r. rowei* here selected (see p. 76) is one of Gregory's three syntypes—E39372, whilst the holotype of *B. r. anglicus* another of his syntypes—75556a. Gregory's third syntype of *Z. rowei*—75556b—is regarded as a paratype of *B. r. anglicus*. Some additional specimens of *Z. costulatus*, *B. r. rowei* and *B. r. anglicus* are now known.

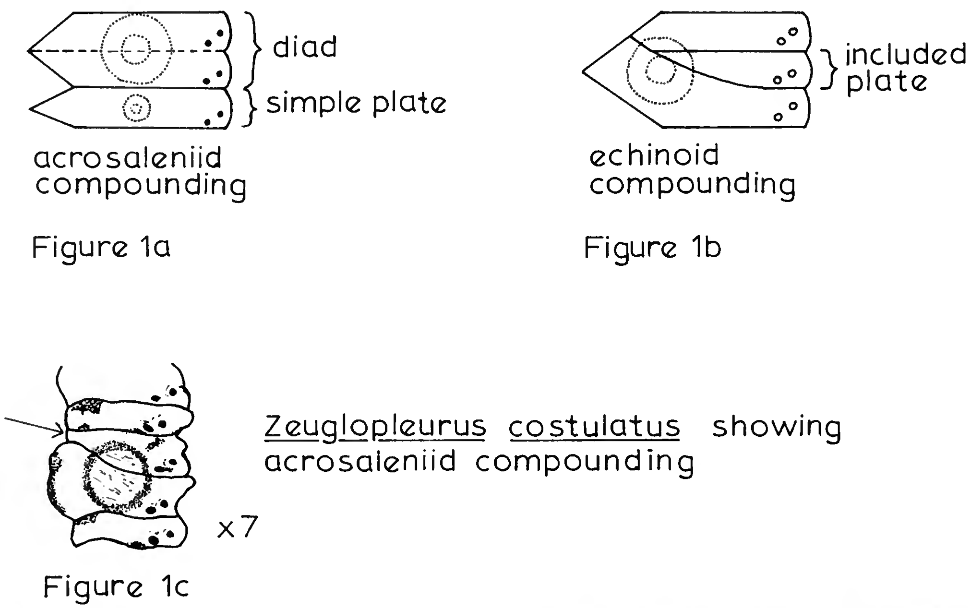


Fig. 1 (a) Diagram to illustrate acrosaleniid compounding. (b) Diagram to illustrate echinoid compounding. (c) Camera lucida drawing to show the kind of acrosaleniid compounding present in an ambulacral plate of *Zeuglopleurus costulatus* (E79244). ↘ indicates component plate having very narrow contact with perradial suture.

The diagnostic characters of the Glyphocyphidae and the Temnopleuridae show that *Zeuglopleurus* and *Boletechinus* belong to neither of these families, and they are therefore placed in the new family Zeuglopleuridae. This should be seen as a plesion within the stem group of the group (Temnopleuridae + Echinoida).

KEY:	GSATC	= Geological Survey of Alabama, Type Collections.
	USNM, USGS	= United States National Museum.
	BM(NH)	= British Museum (Natural History). The prefix to registered numbers is E, except for specimens in very old collections.
	GSM	= Geological Survey Museum (now British Geological Survey).

Systematic descriptions

Superorder **ECHINACEA** Claus, 1876

Order **TEMNOPLEUROIDA** Mortensen, 1942

Family **ZEUGLOPLEURIDAE** nov.

TYPE GENUS. *Zeuglopleurus* Gregory 1889: 494–495.

DIAGNOSIS. Tubercles imperforate, crenulate; test sculptured along plate margins and around secondary tubercles; ambulacra compounded in the acrosaleniid manner; ocular plates I and V insert; periproct elongate, with large suranal plate(s) included in the disc; gill slits shallow. Family currently includes *Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*.

RANGE. Upper Cretaceous of Europe and North America.

DISCUSSION (Figs 2a, 3, 12). Cooke in his diagnosis of *Boletechinus* (1955: 93) was uncertain of its taxonomic position, but he excluded it from the Phymosomatidae because *Orthocyphus*, to which *Boletechinus* bore a resemblance, was dicyclic. He noted also the similarity between *Boletechinus* and '. . . some of the primitive Arbaciidae . . .', the genera having '. . . large basal tubercles . . .'. However, the arbacioids have non-crenulate tubercles and different plate compounding (see Jensen 1981: 55). Cooke's third suggestion was that the genus belonged to the Temnopleuridae as it had a '. . . coarse surface and indented sutures . . .'.

Mortensen (1943: 64) said that, assuming the description and figures by Gregory were representative, *Zeuglopleurus* was an aberrant glyphocyphid because it had the glyphocyphid characters of an 'elongate apical system . . .', and '. . . apparent diadematoid ambulacral structure . . .', but that it was aberrant in having imperforate tubercles. Observations herein of the holotype of *Zeuglopleurus costulatus* show acrosaleniid compounding, verging towards echinoid style compounding, and not the echinoid compounding implied by its inclusion with the Temnopleuridae in the *Treatise* (Fell 1966: U426), and by Mortensen (1943: 67). Mortensen also examined *Z. colleti* by grinding down part of an ambulacrum and concluded that the compounding is echinoid. If this is the case, then *Z. colleti* is not a *Zeuglopleurus* but a temnopleurid as defined in the *Treatise*.

In an attempt to place *Zeuglopleurus* and *Boletechinus* in their correct taxonomic position it is necessary to consider the Glyphocyphidae and Temnopleuridae (see Fig. 12, cladogram, p. 87).

Most glyphocyphids are classified in the *Treatise* as having characters which include acrosalenid plate compounding, apical disc either monocyclic or with ocular plates I and V insert, and perforate tubercles. The *Treatise* also includes in the glyphocyphids genera which do not have all the glyphocyphid characters; examples are *Echinopsis* which has echinoid compounding, and *Progonechinus* which has echinoid compounding and apparently non-crenulate, imperforate tubercles (but this appearance is questioned by Mortensen as being caused by the preservation of the fossil).

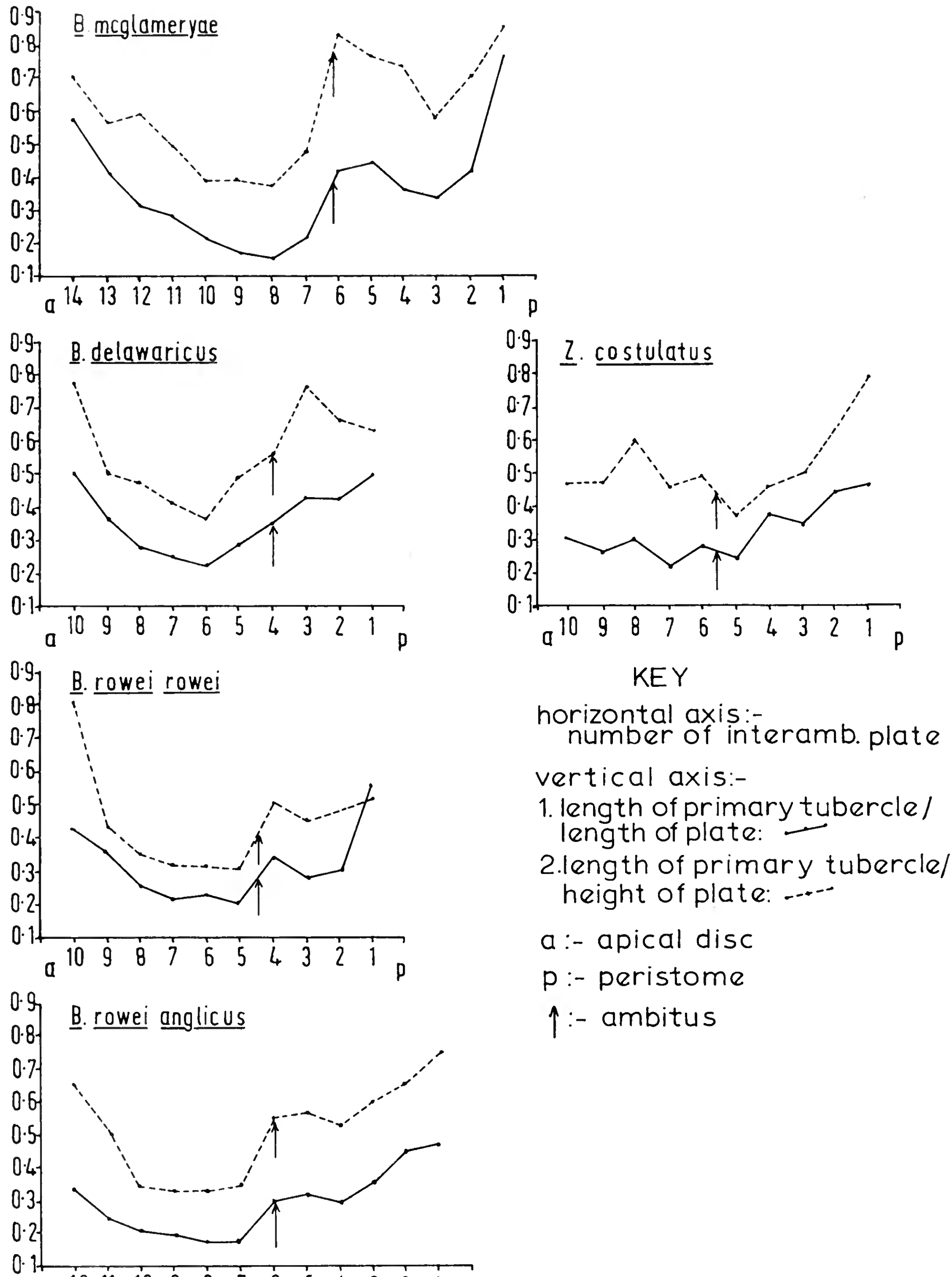

B. mcglameryae
B. delawaricus
Z. costulatus
B. rowei rowei
B. rowei anglicus
0·1 0·2 0·3 0·4 0·5 0·6 0·7 0·8 0·9
a 14 13 12 11 10 9 8 7 6 5 4 3 2 1 p
a 10 9 8 7 6 5 4 3 2 1 p
a 12 11 10 9 8 7 6 5 4 3 2 1 p
KEY
horizontal axis:- number of interamb. plate
vertical axis:-
1. length of primary tubercle/ length of plate:
2. length of primary tubercle/ height of plate:
a :- apical disc
p :- peristome
:- ambitus

Figure 2a

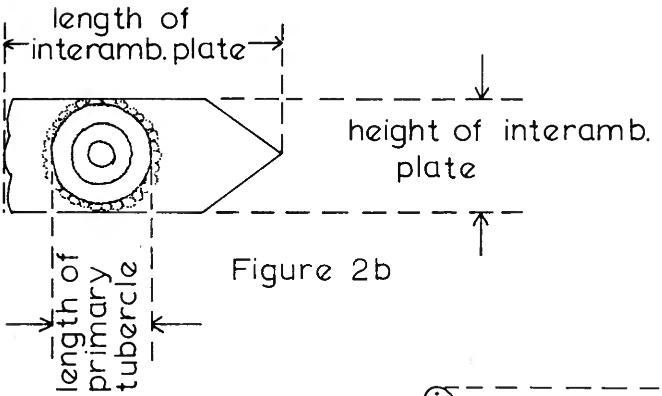


Figure 2b

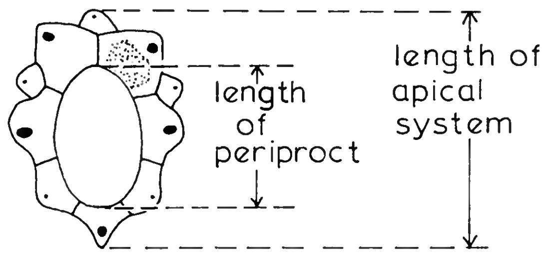


Figure 2c

Fig. 2 (a) Graphs to show the abrupt increase in the size of the primary tubercles at the ambitus for the holotype of each species, with the following data plotted:

$$\frac{\text{length of primary tubercle}}{\text{length of interambulacral plate}} \text{ plotted against the number of the plate, and}$$

$$\frac{\text{length of primary tubercle}}{\text{height of interambulacral plate}} \text{ plotted against the number of the plate.}$$

(b) Diagram to illustrate the measurements of an interambulacral plate.
(c) Diagram to illustrate the measurements of the apical disc.

The characters which currently unite the temnopleurids as classified in the *Treatise* include imperforate tubercles and echinoid plate compounding. Most temnopleurids have dicyclic apical discs, but some have one or more ocular plates insert. The compounding of the ambulacral plates is generally held to be of echinoid type, but illustrations of compounding given by Mortensen and others suggest that this may not always be the case, and that diadematoid or acrosaleniid compounding may occur, for example as in *Paratrema* (Mortensen 1943: 45, fig. 42b), *Hypsiechinus* (1943: 45, fig. 42a), and *Lamprechinus* (1943: 337, figs 195a, b). Further research is needed to check this.

The most characteristic features to distinguish the family Zeuglopleuridae are: ocular plates I and V insert; tessellation into the apical disc of one or more large suranal plates. In other respects the family resembles some of the more primitive members of the Temnopleuridae in that it has imperforate tubercles and prominent sculpturing of the test, but not properly developed echinoid plate compounding. So far, three or four genera have been recognized as belonging to the Zeuglopleuridae—*Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*. According to A. B. Smith (personal communication, and in preparation) the type species of *Glyptocyphus*, *G. difficilis*, has ocular plates I and V insert and large suranal plates included in the apical disc. It has a sculptured test, and plate compounding which is acrosaleniid but which is irregular in its development, even in the same specimen. All these characters

justify including the genus in the new family. The type species of *Echinocyphus*, *E. tenuistriatus*, has a sculptured test, and plate compounding which is acrosaleniid and regularly developed. The apical disc is unknown, but if it should prove to have ocular plates I and V insert, the genus will probably belong to the Zeuglopleuridae. Revision of the Temnopleuridae as defined in the *Treatise* may reveal more members of the Zeuglopleuridae.

The synapomorphies of *Zeuglopleurus* and *Boletechinus* are those of the Zeuglopleuridae, but the abrupt increase in the size of the primary tubercles at the ambitus of *Boletechinus* differs from the steady increase in size of the primary tubercles of *Zeuglopleurus*.

The difference between acrosaleniid compounding and echinoid compounding can be very slight and may depend on whether there is a demiplate present or not. In the case of acrosaleniid compounding all components of a compound plate touch the perradial suture, whereas an echinoid compound plate has one or more demiplates present. In *Zeuglopleurus* (for example, E79244, Fig. 1c) the area of contact with the perradial suture by one component plate is very narrow indeed. It seems likely that close examination of the compounding of some temnopleurids will also show a similar narrow contact with the perradial suture.

Although most temnopleurids have many periproctal plates, some have a few large periproctal plates which are incorporated into the structure of the apical disc. A single large plate was present in *Boletechinus* (see Fig. 10, p. 79) and, although none are preserved, one or more large plates were probably present in *Zeuglopleurus* as is suggested by the angular, elongated periproct with facets for the attachments of periproctal plates (see Fig. 11d, p. 83). Acrosaleniids, as well as having acrosaleniid plate compounding, have large suranal plates tesselated into the apical disc, suggesting the possibility that the Selenioida form the sister group of the Zeuglopleuridae.

It is also interesting to note that where there appears to be acrosaleniid compounding in members of the Temnopleuridae the periproctal plates are reduced in number and increased in size, but where the compounding is certainly echinoid, the periproctal plates are more numerous and much smaller (see text-figures by Mortensen, 1943).

To summarize, with reference to the cladogram (Fig. 12, p. 87), the Glyphocyphidae and the Zeuglopleuridae are both plesions within the stem group of the Temnopleuridae + Echinoida (= Camarodonta *sensu* Jackson 1912: 183).

CONCLUSION. The Zeuglopleuridae, at present comprising *Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*, form a plesion in the stem group of Temnopleuridae + Echinoida. The autapomorphies of the new family include: ocular plates I and V insert; elongate periproct with large suranal plate(s).

Zeuglopleurus is readily distinguished from *Boletechinus* by the abrupt increase in size of the primary tubercles at the ambitus of *Boletechinus*. Further research is necessary to determine whether any other genera of the Temnopleuridae should be included in the Zeuglopleuridae, and examination of the Glyphocyphidae and Temnopleuridae may show that there are more natural groupings than just three.

Genus ***BOLETECHINUS*** Cooke 1955

TYPE SPECIES. *Boletechinus mcglameryae* Cooke 1955.

DESCRIPTION. *Shape*: A small zeuglopleurid with a hemispherical test, slightly higher at the anterior end than at the posterior end.

Apical System: 1) Ocular plates. Ocular plates I and V are insert and are between 15% and 25% larger than oculars II, III, and IV. There is an elongated M-shaped margin next to ambulacra I and V and an ocular pore just adoral to the centre of the M. Oculars II, III, and IV have less elongate M-shaped margins next to ambulacra II, III and IV, with the ocular pore just adoral to the centre of the M. All the ocular pores are perradial in position. The ornament consists of several small tubercles.

2) Genital plates and madreporite. These form the anterior, lateral, and posterior-most margins of the periproct. Genital plate 5 is the smallest and has the shape of a short stubby

boomerang, has an interradial pore, and a slight swelling of the adoral margin into the periproct. The genital pores of plates 1, 3 and 4, and of plate 2 when recognizable, are very slightly anteriorly adradial in position. The madreporic part of plate 2 is a prominent swelling and is perforated by many tiny pores. The ornament of genital plates 1–4 consists of tubercles or pits, whilst plate 5 lacks any large ornament.

3) Periproct. This is elongated along the anteroposterior axis. The longer dimension is usually between 15% and 25% greater than the shorter. The rim of the periproct formed by oculars I and V and genital plates 1–4 is either raised or level with the surface of the test, whilst the rim formed by genital plate 5 is level with the surface of the test or very slightly lower.

Ambulacra: These are straight, taper adapically and adorally and are widest at the ambitus. There are between about 4 and 12 simple plates, counting from the apical disc adorally, and then up to about 9 compound plates to the peristome. The plates are compounded in the acrosaleniid manner. The pore pairs are in monoserial columns, and are similar, and oblique so that the adradial pore is more adapical than the perradial pore. The pores of a pair are separated by a thin wall, and the pair is surrounded by a low wall, with a gap at the perradial adoral margin. The ornament of the ambulacra consists of primary and secondary tubercles and sculpturing or excavation of the test.

The primary tubercles each consist of a low, convex, circular boss, a parapet with 10 to 14 crenulations, a short neck and an undercut, imperforate, hemispherical mamelon. If a column is followed from the apical disc adorally, the size of the primary tubercles is seen to increase abruptly near the ambitus.

Secondary tubercles have low convex bosses with small mamelons. The tubercles vary in size and give a granular appearance to the ambulacra.

Sculpturing of the ambulacra occurs along plate margins and around the tubercles, sometimes giving a rough appearance to the test.

Interambulacra: These taper adorally and adapically and are widest at the ambitus. The ornament consists of primary and secondary tubercles and sculpturing or excavation of the test. There are up to 14 plates per interambulacrum in each column.

The primary tubercles and the secondary tubercles of the interambulacra have a similar structure to those of the ambulacra, with up to 14 crenulations on the primary tubercles. If a column is followed adorally from the apical disc, the size of the primary tubercles is seen to increase abruptly near the ambitus. The sculpturing occurs along plate margins and around the tubercles, sometimes giving a rough appearance to the test.

Peristome: This is decagonal and has shallow gill slits.

RANGE. Upper Cretaceous of Europe and North America.

REMARKS. The abrupt increase in the size of the primary tubercles at the ambitus of *Boletechinus* readily distinguishes the genus from *Zeuglopleurus*, whose tubercles increase in size gradually (Figs 2a, b, 3a–f).

Boletechinus mcglameryae Cooke

Figs 2a, 3a–f, 4a–f

1955 *Boletechinus mcglameryae* Cooke: 93; pl. 28, figs 11–16; text-fig. 4.

DIAGNOSIS. A *Boletechinus* whose test from ambitus adapically has a very granular appearance, with secondary tubercles close together over the surface of each plate. Plate boundaries not very distinct, partly obscured by ornament. Two thin, almost parallel ridges form inverted V on adoral sides of plates, prominent above ambitus, less distinct adorally. Primary tubercles from ambitus to oral surface relatively small. Periproct angular, slightly elongated.

MATERIAL. Holotype: GSATC 108, from the Cretaceous, Maastrichtian, Prairie Bluff Chalk; from 2 miles north of Livingstone, Sumter County, Alabama (Figs 4a–f).

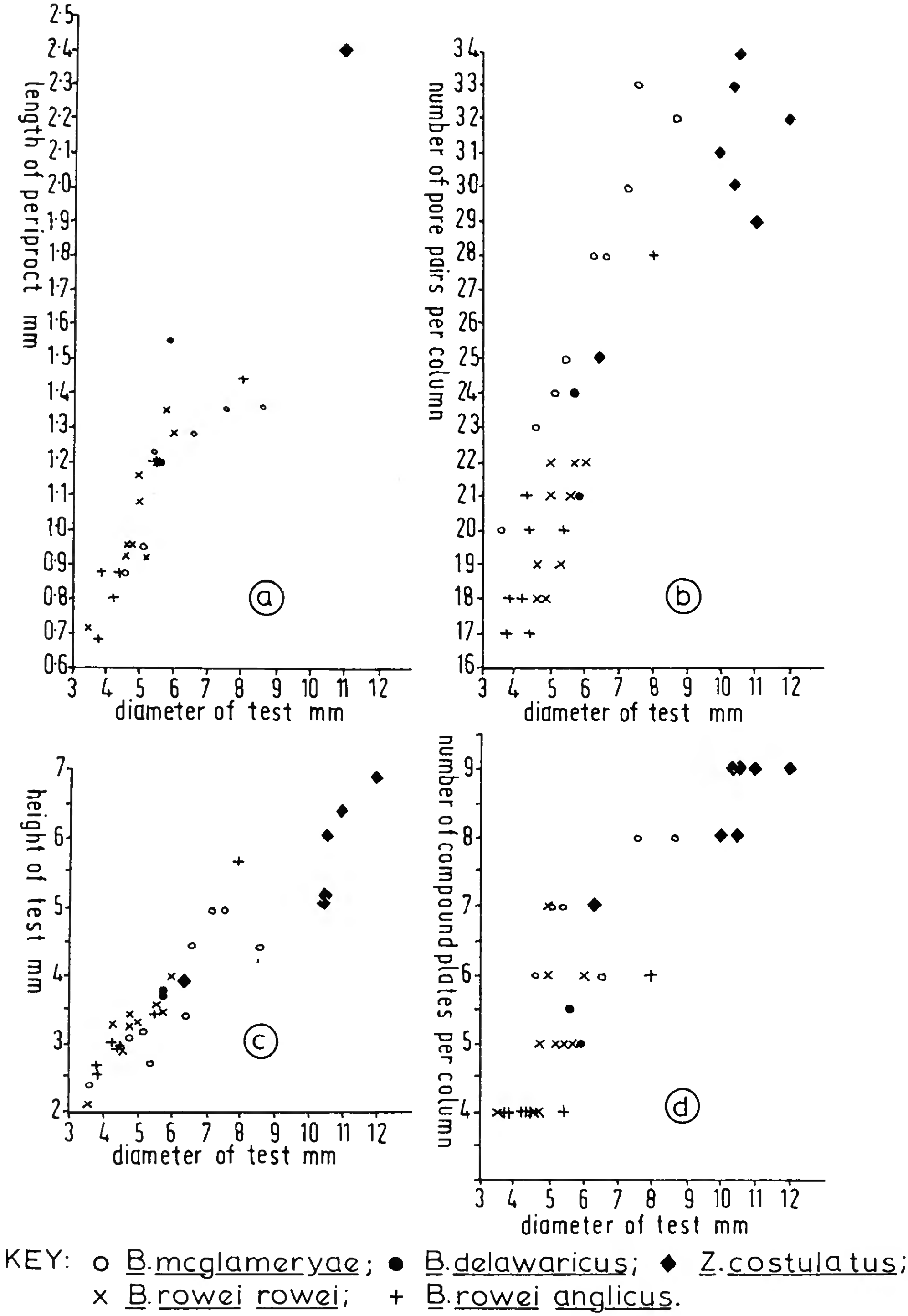

length of periproct mm
diameter of test mm
number of pore pairs per column
diameter of test mm
height of test mm
diameter of test mm
number of compound plates per column
diameter of test mm
KEY: o B.mcglameryae; ● B.delawaricus; ◆ Z.costulatus;
× B.rowei rowei; + B.rowei anglicus.

Figure 3

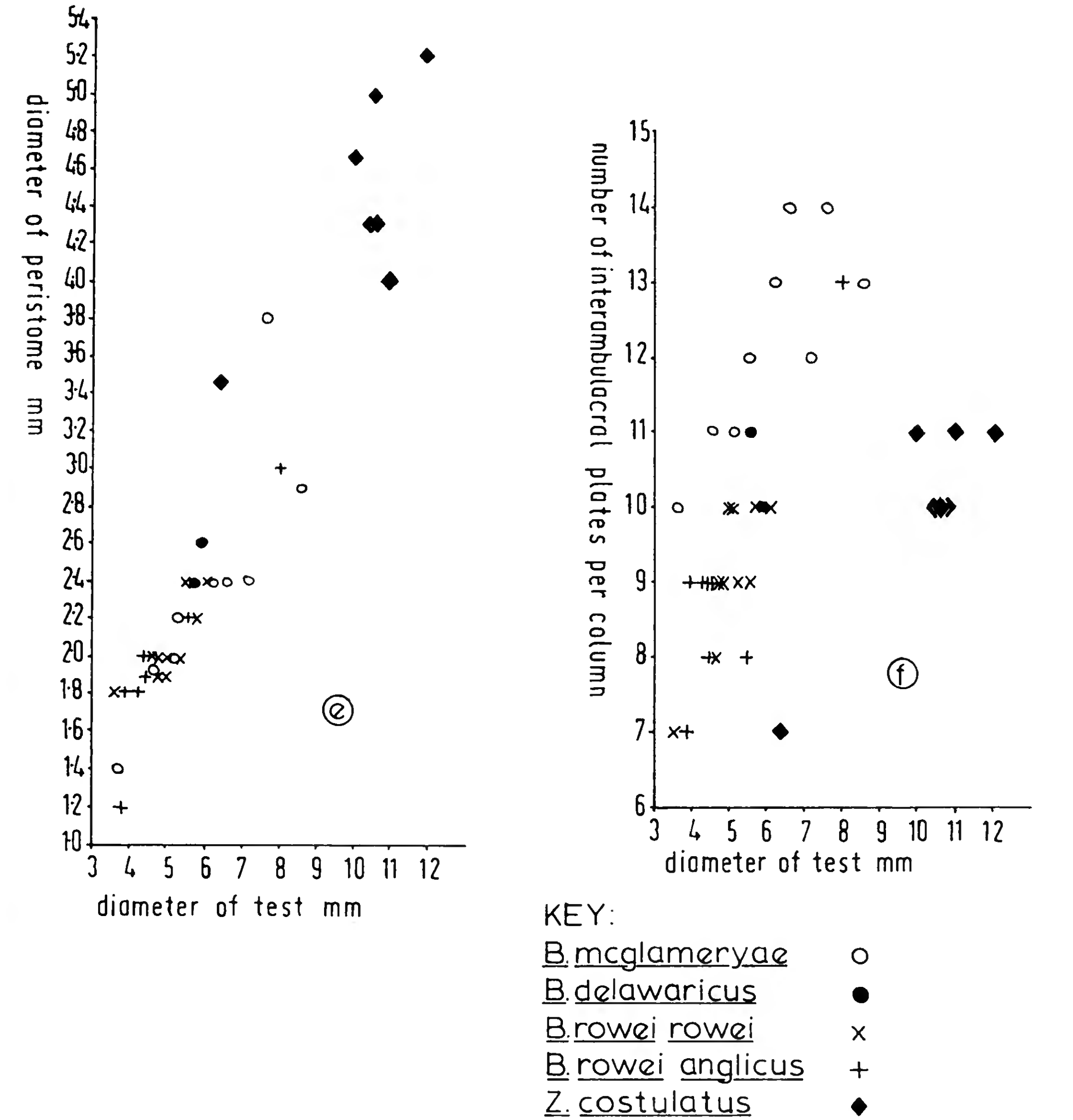


Figure 3

Fig. 3 (a) Graph to show the close similarity between species of *Boletechinus* when the length of the periproct is compared with the diameter of the test. *Zeuglopleurus costulatus* (holotype) falls outside the *Boletechinus* cluster. (b) Graph compares the diameter of the test with the number of pore-pairs per column for each species. *Z. costulatus* falls outside the *Boletechinus* cluster. (c) Graph compares the diameter of the test with its height for each species. *Z. costulatus* is separated from the *Boletechinus* cluster. (d) Graph compares the diameter of the test with the number of compound plates per column for each species. *Z. costulatus* is separated from the *Boletechinus* cluster. (e) Graph compares the diameter of the test with the diameter of the peristome for each species. *Z. costulatus* falls far outside the *Boletechinus* cluster. (f) Graph compares the number of interambulacral plates with the diameter of the test for each species. *Z. costulatus* is separated from the *Boletechinus* cluster. N.B. All the graphs illustrate the difficulty of separating the species by comparing measurements and numbers of components of the test.

Paratypes: GSATC 108 from the same locality; USNM 108689 (figured by Cooke 1955: pl. 28, figs 14–16) and USGS 18636 from the same locality.

SHAPE. The test is hemispherical, slightly lower at the posterior end. Some specimens are flattened so that the test is almost discoidal. Dimensions of the holotype (mm): diameter of test 7·6, height of test 4·9, diameter of peristome 2·8.

PRESERVATION. The holotype is uncrushed, slightly abraded and is filled with a pinkish grey matrix. The GSATC paratypes are filled with a cream-coloured matrix, and are less abraded. The apical disc of one specimen has been pathologically displaced towards ambulacrum I and interambulacrum 1, thereby elongating the adapical ambulacra and interambulacra of the opposite side, and shortening those on the same side. There is also a slight indentation of the test at interradius 5 in this specimen. The USNM specimen figured by Cooke (1955) is uncrushed, slightly abraded, and a small part of interambulacrum 3 adoral to the ambitus is missing. The specimen is filled with a cream-coloured matrix. The other USNM specimens are undamaged and have a pale grey matrix.

APICAL SYSTEM (Fig. 4f). 1) Ocular plates. Ocular plates I and V are about 25% longer than oculars II–IV. The outline of oculars I and V is approximately hexagonal, with a very broad V-shaped periproctal margin. The M-shaped margin has small pits on the surface. Oculars II–IV each have a rounded M-shaped margin, and have an ocular pore situated near the adoral perradial margin of each plate.

Ornament consists of three or more tubercles on each plate; on oculars I and V they are present along the periproctal edge of the plate; on oculars II–IV they are grouped together at the periproctal end. There are also many small pits present on the non-tubercular parts of the oculars.

2) Genital plates and madreporite. The periproctal margins are each gently concave. Plates 1 and 4 are elongated at their anterior ends, and have five other sides. The madreporite is formed on the anterior two-thirds of genital plate 2. Genital plate 3 has the same outline shape as genital plate 2, but is about three-quarters of the size. The posterior-most part of the periproct formed by genital plate 5 has an outline of a very elongate and angular U, so that this margin and the adjacent margins of oculars I and V appear scalloped. The genital pores of plates 1, 3 and 4 are quite large and slightly oval, and with the long axis interradial. Genital plate 5 has a circular pore near the adoral margin.

The ornament of genital plates 1–4 consists of a few small tubercles and fairly deep pits. Genital plate 5 has no ornament. There is a single pit between genital plates 1 and 2, 2 and 3, and 3 and 4. There is no pit between genital plate 5 and oculars I and V. The elongated appearance of genital plate 5 is due to its two long margins being straighter than the equivalent, convex, margins of the other genital plates. These two straight sides meet at a sharper angle than do their equivalents in the other genital plates. The dimensions of genital plates in the holotype are given in Table 1.

Table 1 Dimensions of genital plates in holotype of *Boletechinus mcglameryae* Cooke. L = maximum length between adradial margins; W = maximum width, periproctal margin to interradius (mm).

Plate	L	W
1	0·76	0·6
2	0·9	0·66
3	0·7	0·64
4	0·72	0·6
5	0·66	0·4

3) Periproct. This has an angular outline, with straight margins at oculars I and V and genital plates 1–4. Genital plate 5 has a V-shaped periproctal margin. The periproct is also elongated along the anteroposterior axis. The paratype figured by Cooke (1955) has a smoother, slightly greater than semicircular outline in the anterior part, and a scalloped outline in the posterior part. The longer dimension is about 20% greater than the shorter in Cooke's figured paratype and about 40% in the holotype. The margin of the periproct is level with the surface of the test, except at genital plate 5 where it is slightly concave.

AMBULACRA (Fig. 4d). The ratios of the width of the ambulacra to the width of the interambulacra of the holotype are:

at the apical disc	1 : 2
at the ambitus	1 : 1·8
at the peristome	1 : 1·5

The pores are circular, similar, and surrounded by a flat rim whose adoral perradial side is partly obscured by the adoral adradial margin of the next adoral plate. The plates are simple from the apical disc to a position just adapical to the ambitus. The succeeding plates are acrosaleniid compounds.

Smaller primary tubercles are present from the apical disc to the ambitus, whilst larger primary tubercles, with about 12 crenulations, occur abruptly at the ambitus together with an abrupt increase in the diameter of the scrobicules. Adorally, the decrease in size is gradual. The secondary tubercles of smaller simple plates are present on the perradial ends of the plates and are approximately the same size as the primary tubercles, whilst on larger simple plates there are two or three secondary tubercles in this position. Adoral to the primary tubercle of the simple plate there is a single tubercle connected to the boss by a small ridge. On the compound plates there are two secondary tubercles and two ridges forming an inverted V-shape on the adoral side of the compound plate. The adoral ends of the ridge join two secondary tubercles on the simple plate between adjacent compound plates. At the ambitus and adorally, the ridges become much less distinct. This arrangement produces a weak, discontinuous rib extending from the apical disc to the larger primary tubercles at the ambitus.

The compound plates with large primary tubercles each have secondary tubercles along the adapical margins and the perradial margins, and the simple plate has a row of secondary tubercles plus a small primary tubercle. Together, a horseshoe-shape of secondary tubercles is formed but without a distinct continuation of the ribs formed adapically.

Sculpturing between adjacent secondary tubercles gives the ambulacra a coarse appearance. The adapical margins of the simple plates on the adapical part of the ambulacra are raised, giving the plates a tilted appearance.

There are between about 5 and 12 simple plates and between about 5 and 9 compound plates to each ambulacral column for tests with diameters between 3·7 mm and 8·7 mm.

INTERAMBULACRA (Fig. 4e). These broaden rather rapidly from the apical disc to the ambitus, then taper gently to the peristome. The adapical margins of the plates are raised slightly above the general surface of the test to give a tilted appearance to the plates.

Each primary tubercle has about 14 crenulations. Secondary tubercles are present as incomplete scrobicular circles on each plate. They are situated along the adradial and interradial margins of the plate, with 4–6 of them along each margin. The secondary tubercles are all about the same size as a small primary tubercle of an ambulacrum. Further secondary tubercules of this size are present along the plate margins.

Between the adoral side of the boss of the primary tubercle and the adapical side of its adoral neighbour there are thin rounded ridges, which form an inverted V-shape with almost parallel sides. The adoral ends of the V are two small secondary tubercles on the adjacent adoral plate. Sometimes a third ridge is present, either adradial or interradial in position. The ridges plus primary tubercles produce on each interambulacrum an appearance of two discontinuous ribs extending from the apical disc to ambitus. At the ambitus the V-shape opens out and the ridges

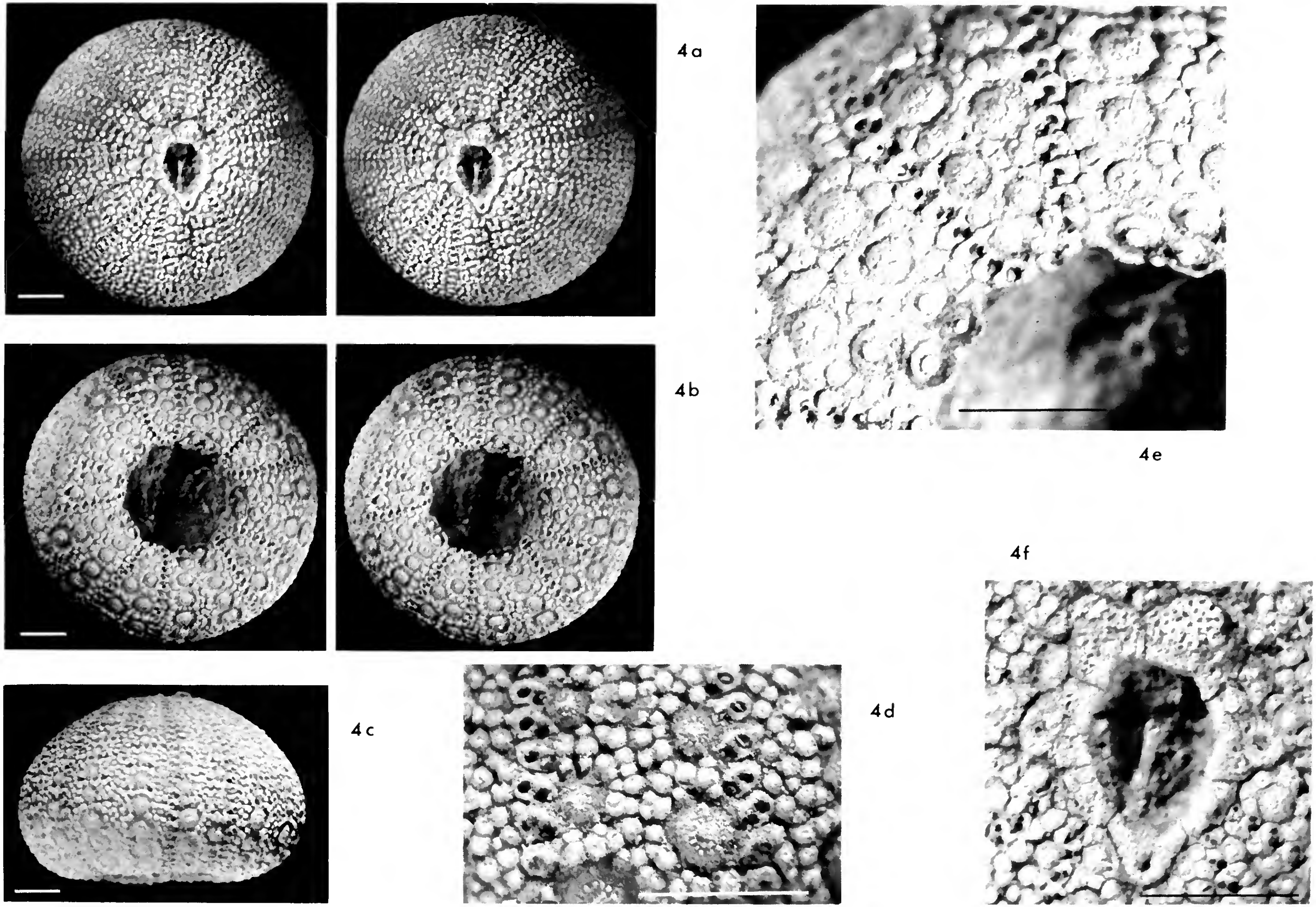


Fig. 4 *Boletechinus mcglameryae* Cooke, holotype GSATC 108. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), side view; (d), close-up of ambulacral ornament; (e), detail of part of the peristome; (f), apical disc. Scale bars 1 mm.

become much reduced in size. The plates are excavated around each secondary tubercle and between the ridges, to give a rough texture to the test.

There are 10–14 plates to each interambulacral column for tests with diameters between 3·7 mm and 8·7 mm.

PERISTOME (Figs 4b, 4e). The diameter of the peristome is about 37% of the diameter of the test, with some primary and secondary tubercles protruding into the peristome.

Boletechinus delawaricus sp. nov.

Figs 2a, 3a–f, 5a–d, 6, 7

DIAGNOSIS. A *Boletechinus* with diamond-shaped depression between adoral edge of one interambulacral primary boss and adapical edge of adjacent interambulacral boss. Depression bordered by divergent adradial and interradial ridges which may enclose an additional ridge consisting of components of both constituent plates. Test with well-defined plate boundaries. Primary tubercles at ambitus and on oral surface relatively large. Periproct oval.

MATERIAL. Three specimens from the Upper Cretaceous, Monmouth Group, Navesink Marl (= Maastrichtian; see Spangler & Peterson 1950: 8), from the Delaware Canal, Delaware, U.S.A., were given by Mr Allan Graffham, owner manager of 'Geological Enterprises' in Oklahoma, to Mr R. Baker who presented them to the British Museum (Natural History) in 1979.

TYPES. Holotype: E76803 (Fig. 5); Paratypes: E76804 (Fig. 7), E76805 (Fig. 6).

PRESERVATION. Two of the specimens are uncrushed but have been slightly abraded. Paratype E76805 has the remains of a membraniporid bryozoan attached to the test.

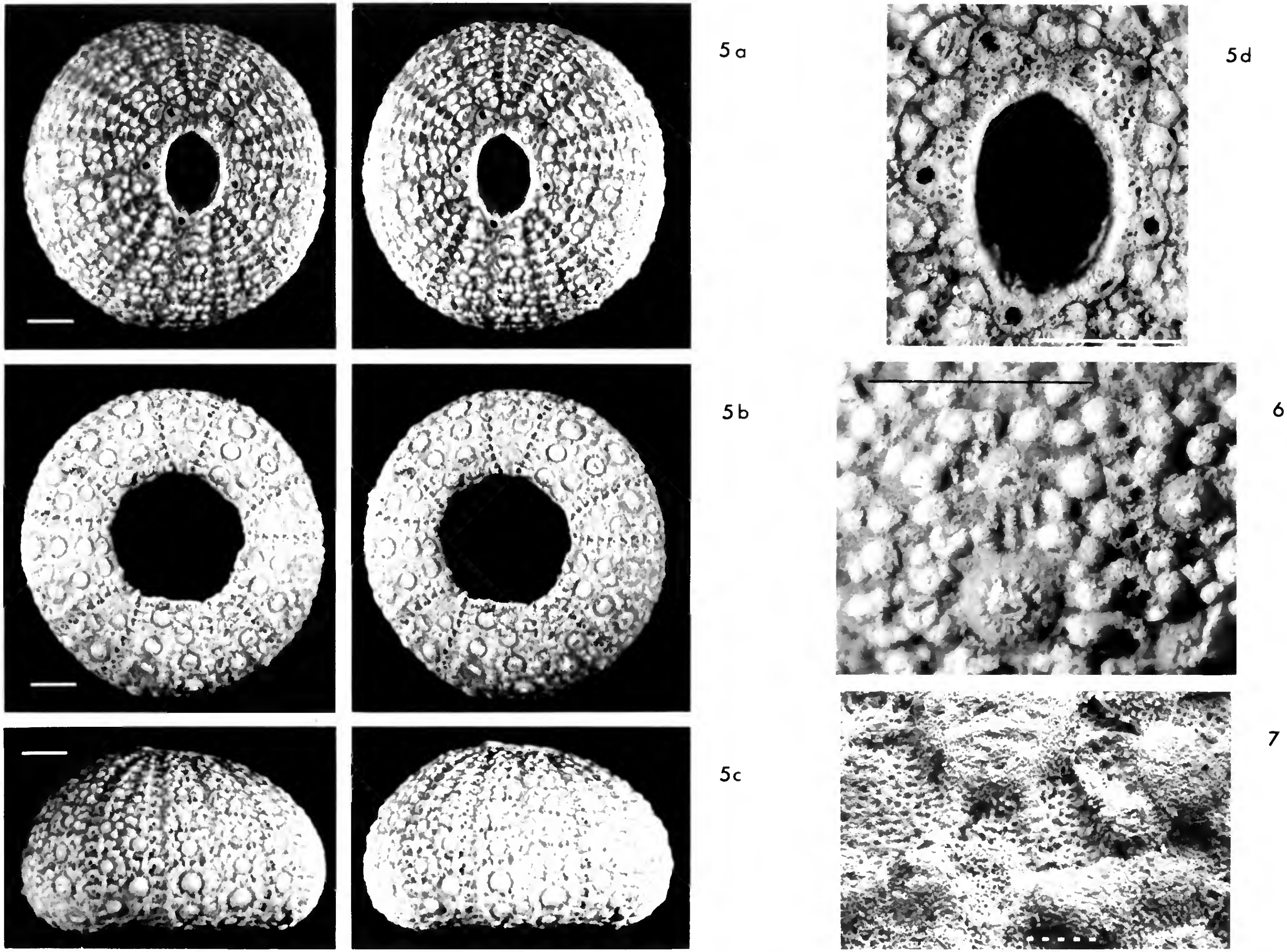
SHAPE. The specimens are approximately hemispherical, with the anterior end slightly higher than the posterior end. There is a circular peristome of moderate size and an elongate periproct with a slightly raised margin.

Table 2 Dimensions (mm) of holotype and paratypes of *Boletechinus delawaricus* sp. nov.

	Diameter	Height	Diameter of peristome
Holotype E76803	5·9	3·7	2·6
Paratype E76804	5·9	3·6	2·3
Paratype E76805	5·7	3·7	2·4

APICAL SYSTEM (Fig. 5d). 1) Ocular plates. Ocular plates I and V are 15–20% longer than ocular plates II, III and IV. The outline of oculars I and V is approximately hexagonal, with a gently concave periproctal margin. The M-shaped margin at ambulacra I and V is flattened. Oculars II, III and IV are approximately pentagonal, and have flattened M-shaped margins. The ornament of each plate consists of a large tubercle adapical to the pore and a few smaller tubercles or granules next to the large tubercles. The details of the ornament of the tubercles have been removed by abrasion. At all the margins except the M-shaped ones there are fine striations perpendicular to the sutures. These striations pass from the base of the tubercles to the margins of the plates, are continuous with those of adjacent genital plates, and run indistinctly onto adjacent interambulacral plates.

2) Genital plates and madreporite. The periproctal margin of each genital plate is strongly concave. Genital plates 1 and 4 are more elongated at their anterior ends, and each has six sides. The elongation of genital plates 1 and 4 makes them asymmetrical in outline, unlike the bilaterally symmetrical outlines of plates 2 and 3. Genital plates 2 and 3 have seven sides. The



Figs 5–7 *Boletechinus delawaricus* sp. nov. Fig. 5, **holotype** E76803. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), apical disc. Fig. 6, paratype E76805. Interambulacral ornament, showing abrupt increase in tubercle size, and the additional ridge in the diamond-shaped depression between adjacent plates. Fig. 7, paratype E76804. S.E.M. photograph to show the diamond-shaped depression between adjacent interambulacral plates. Scale bars 1 mm (Fig. 7, 0·1 mm).

ornament of genital plates 1, 3 and 4 consists of a single large tubercle close to the middle of the periproctal margins, and several well-defined, small, shallow pits are present near the plate margins bordering ocular plates II, III and IV. Also present are fine striations, perpendicular to these same margins, and continuous with the striations of adjacent ocular plates.

Each genital pore is large, and fairly close to the edge of the plate. The madreporic part of genital plate 2 is perforated with many holes a little less in diameter than the genital pores. The ornament of genital plate 2 consists of the fine striations, as present in genital plates 1 and 4, but there are fewer shallow pits. There is a single large tubercle which has become partly incorporated into the raised madreporic part of the plate.

Genital plate 5 has an interradial genital pore equidistant from the posterior margins and the periproctal margin. There is no conspicuous ornament. The periproctal margins of the genital and ocular plates have rounded edges.

Table 3 Dimensions of genital plates in holotype of *Boletechinus delawaricus* sp. nov. L = maximum length between adradial margins; W = maximum width, periproctal margin to interradial suture (mm).

Plate	L	W
1	0·7	0·4
2	0·7	0·6
3	0·8	0·6
4	0·75	0·5
5	0·7	0·3

3) Periproct. This has the outline of an elongated pentagon with curved sides. The longer dimension, along the anteroposterior axis, is about 25% greater than the shorter dimension from genital plate 1 to genital plate 4. The margin of ocular and genital plates is slightly raised except at genital plate 5 which is level with the surface of the test.

AMBULACRA (Fig. 6). The ratios of the width of the ambulacra to the width of the interambulacra of the holotype are:

at the apical disc 1 : 2·5
at the ambitus 1 : 1·4
at the peristome 1 : 1·7

The adapical sides of the plates are raised slightly to give a tilted appearance. The first 4 to 12 plates from the apical disc adorally are simple, then 3 to 5 acrosaleniid compound plates continue to the peristome.

The pore-pairs of each plate—both simple and compound—are situated on an area whose outline is approximately square. They are oblique, circular, similar, and each pair is separated from its neighbour by a thin wall. The perradial pore is open at its adoral margin.

Larger primary tubercles are low, with between about 10 and 14 coarse crenulations. The tubercle is central in position on each compound plate and covers most of it. Smaller primary tubercles are situated on the centre of each of the simple plates adapical to the ambitus. On the first few compound plates the adapical quarter or third of the boss overlaps the adoral margin of the adjacent adapical plate and together with adoral and adapical secondary tubercles, and the primary tubercle of simple plates, form interrupted ridges adapical to the ambitus. Single secondary tubercles occur on the perradial margins of the simple plates, several secondary tubercles occur along the perradial margins of the compound plates—usually two on the adapical and two on the adoral perradial margins—and three secondary tubercles are present on the simple plates between compound plates.

Broad grooves extend from between each secondary tubercle to the boss of the primary tubercle. The sutures between the simple plates of the ambulacra adapical to the ambitus are well defined, whilst those between the compound plates and simple plates are less well defined. The definition is enhanced by the slight excavation along the margins of each plate, and between each simple plate and each compound plate adjacent to a simple plate there is a triangular pit on the adapical margin. The apex of the triangle is adoral, the base extends from the adradial margin of the plate to the perradial part of the 'square' containing the pore-pairs.

INTERAMBULACRA (Figs 6, 7). The adapical margins of the plates are slightly raised to give a tilted appearance to each plate. The larger primary tubercles have between 11 and 14 coarse crenulations. The secondary tubercles form scrobicular arcs, and appear as small hemispheres about the same size as the mamelon of a primary tubercle, and are close together. There are usually three of them along each adradial and interradial margin, and some near the adradial adapical edges of the plates. Between adjacent secondary tubercles is a very shallow depression extending to the base of the primary boss, giving the scrobicule a slightly crenulated appearance. On the adapical and adoral sides of each plate there are two ridges which radiate from the base of the boss and meet the ridges of the adjacent plates adorally and adapically. The ridges enclose a small diamond-shaped depression (Fig. 7). In paratype E76805 additional ridges are frequently included within the diamond shape and are continuous from the adapical to the adjacent adoral plate, and occur from the ambitus adorally (Fig. 6). Seen from a distance, the ridges and primary tubercles give the appearance of two discontinuous ribs along the interambulacral columns, less well defined on the oral surface.

The sutures between each plate are well defined and are very slightly excavated. The interradial suture is also excavated and tapers very gradually to the oral surface, close to the peristome. There are about 10 or 11 plates in an interambulacral column, with a test diameter of between 5·7 mm and 5·9 mm.

PERISTOME (Fig. 5b). The diameter is about 43% of the diameter of the test, and the outline is pentagonal with rounded angles. The five straight sides are interambulacral and the rounded angles are ambulacral. The holotype has all the apophyses preserved and auricle IVb, but the other auricles have been broken off at their bases. The auricle is a U-shaped structure which is tilted upwards away from the peristome. It is short and has rounded tips, and shows the retractor-muscle scars. The apophyses form lower, convex swellings with distinct sutures at their adradial margins with the auricles. The perignathic girdle of the paratype E76805 is obscured by matrix.

Boletechinus rowei (Gregory)

1900 *Zeuglopleurus rowei* Gregory: 353–354, figs 1–4.
1943 *Zeuglopleurus rowei* Gregory; Mortensen: 352–353.

DIAGNOSIS. A *Boletechinus* with very oblique pore-pairs. Two ridges composed of coalesced secondary tubercules on adoral side of plates extend from primary boss to adoral scrobicular tubercles. Primary tubercles from ambitus to oral surface relatively small. Periproct slightly elongated.

There are two sub-species, *B. rowei rowei* and *B. rowei anglicus* subsp. nov.

SHAPE. The shape is circular, or a rounded pentagon; approximately hemispherical, with the anterior end slightly higher than the posterior end. Periproct is slightly elongated; peristome is decagonal.

APICAL DISC. 1) Ocular plates. Oculars I and V are about 25% longer than oculars II–IV. The periproctal margins of oculars I and V are concave, slightly angular. The outline of oculars I–V is angular, with plates II–IV approximately pentagonal. The ornament varies between the subspecies. The shape of the apical disc is slightly ovoid, with the elongation along the antero-posterior axis.

2) Genital plates and madreporite. The non-periproctal margins are straight, and convexly rounded at the interradius. The genital pores are quite large, and are situated in an approximately circular raised area composed of a few coalesced tubercles. Ornament consists of several granular tubercles about the same size as the secondary tubercles elsewhere on the test. Between the tubercles and around the raised circular area containing the genital pore, the test is sculptured to a greater or lesser amount. Genital pore 5 has a slightly raised rim which bulges into the periproct. The periproctal margins of genital plates 1–4 have the outline of a broad, asymmetrical V-shape, the longer side anterior. The periproctal margin of genital plate 5 is a regular V-shape, with a slight bulge into the dip of the V. Along the periproctal margins there are a few quite large tubercles with sculpturing between them. The madreporite is an irregular swelling with many perforations which may obscure the position of the genital pore. When the genital pore of plate 2 is obvious, it is situated on a low, unornamented part of the plate.

3) Periproct. The periproct is slightly elongated anteroposteriorly, and is between 15% and 25% longer than wide. It varies in outline from a slightly elongated circle to an elongated pentagon. At the junction between one marginal plate and its neighbour there is a slight swelling into the periproct, giving it an undulating outline. This is better seen in a periproct with pentagonal outline.

AMBULACRA. The ambulacra are composed of both simple and compound plates. There are between 5 and 10 simple plates and between 3 and 7 compound plates in each column for tests of diameters between 3·8 mm and 8 mm. Simple plates occur from the apical disc adorally, and compound plates from just apical of the ambitus to the peristome. The pores of a pair are similar and very oblique—the adradial pore is almost directly adapical to the perradial pore. They are slightly elongated, almost teardrop-shaped, with the long axis of the adapical pore approximately parallel to the transverse suture, and the long axis of the perradial pore obliquely perradial–adradial. The pores are sunken into the plate and are separated from each other by a low wall or ridge. A rim around each pair of pores is much taller at the adradial edge than diagonally opposite at the perradial edge, and gives an obliquely tilted appearance to that part of the plate, almost to isolate it from the rest of the plate.

The primary tubercles have up to 14 crenulations, depending on the size of tubercle. Secondary tubercles have a granular appearance and are approximately the same size as the mamelon of a large primary tubercle. On the most adapical plates there is one secondary tubercle near the perradial edge of the plate, but elsewhere there are two. Further adorally, on small diad compound plates, secondary tubercles form small clusters around primary tubercles. On larger compound plates, secondary tubercles form adradially incomplete, non-confluent scrobicular circles, separated by the simple plate bearing its own primary and secondary tubercles. On compound plates from the ambitus adorally, the scrobicules may be excavated from the boss to the secondary tubercles to give a spoked effect of radiating ridges. There are also many extrascrobicular tubercles.

INTERAMBULACRA. The width of an interambulacrum is about half as much again as an ambulacrum. The ratio of the width of each interambulacrum at the apical disc, ambitus and peristome is 1 : 2·4 : 1. The primary boss has up to 14 crenulations, depending on size. Secondary tubercles are approximately the same size as the mamelon of a larger primary tubercle, and have a granular appearance. The secondary tubercles form contiguous scrobicular arcs which are approximately semicircular, and are also present elsewhere on the plate as numerous extrascrobicular tubercles, sometimes forming additional though incomplete arcs. The scrobicular tubercles adapical to the ambitus are situated very close to, or are in contact with, the primary boss. At the ambitus, at the abrupt increase in the size of the primary tubercles, and adorally, there is a distinct but narrow scrobicule between the primary base of the primary boss and the scrobicular tubercles, frequently with excavations in the surface from boss to secondary tubercle, forming a spoked appearance to the plate. The prominence of the spoked effect varies with the subspecies. There are between 7 and 13 interambulacral plates per column for tests with diameters of between 3·8 mm and 8 mm.

PERISTOME. The ratio of the width of the ambulacra to the width of the interambulacra at the peristome varies from 1 : 1·2 to 1 : 1·9 (mean 1 : 1·5), depending on size of test. The gill slits have low rims around their edges, and these extend onto the outer surface of the interambulacra. The apophyses are thick ridges; the auricles are short pegs which are not joined, and have distinct retractor-muscle scars.

Boletechinus rowei rowei (Gregory)

Figs 2a, 3a–f, 8a–e

1900 *Zeuglopleurus rowei* Gregory: 353–354, figs 1–3.
1943 *Zeuglopleurus rowei* Gregory; Mortensen: 352.

DIAGNOSIS. A *Boletechinus* whose plate boundaries are obscured by secondary tubercles, which give a granular stellate appearance to the ornament adapical to the ambitus. Stellate ornament not present from ambitus adorally.

LECTOTYPE. E39372 (Fig. 8), herein selected from the three syntypes of *Zeuglopleurus rowei* Gregory. This specimen is from the Santonian of Westgate, Thanet Coast, Kent. The other two syntypes (now paralectotypes), 75556a and 75556b, are referred to the new subspecies *anglicus* (see p. 78; also p. 60).

OTHER MATERIAL. E39374–5 from the Santonian, *Uintracrinus* band of the Thanet Coast, Kent; E39804 from the Santonian, *Marsupites* band of south of High Stacks, Flamborough Head, Yorkshire; E39807 from the Lower Campanian, *quadratus* Zone, from a pit $\frac{1}{2}$ mile NW of Wells, Norfolk; GSM 118260 from the Santonian, *coranguinum* Zone, 0–0·5 m above Bedwell's Columnar Band, West Ramsgate, Thanet, Kent; GSM 11861–2 from the Santonian, mid-*Uintacrinus* Zone, at or just above level of *Hagenowia* horizon, Epple Bay, Birchington, Thanet, Kent; GSM 118263 from the Santonian, *coranguinum* Zone, 3·5–4 m below Bedwell's Columnar Band, West Ramsgate, Thanet, Kent; GSM 118264–5 from the Santonian, *coranguinum* Zone, in basal 0·5 m of Bedwell's Columnar Band, North Foreland, north of Broadstairs, Thanet, Kent. All GSM specimens are from the A. S. Gale collection.

PRESERVATION. The specimens are well preserved except for E39807 which is abraded and incomplete, and also partly enclosed in flint.

SHAPE (Figs 3a–f). The dimensions of the lectotype are: diameter of test 5·8 mm; height of test 3·9 mm; diameter of peristome 2·2 mm.

APICAL SYSTEM (Fig. 8d). 1) Ocular plates. Ornament consists of three large tubercles along the periproctal margin, and another near the margins next to interambulacral columns 1a and 4b. This tubercle is situated on a part of the plate anterior to the perradius. About three large tubercles are present along the adapical margins of oculars II–IV. These tubercles are very close together, forming a tall wall adapical to the ocular pore. All oculars are lightly sculptured between the tubercles.

2) Genital plates and madreporite. The ornament of genital plate 3 consists of several tubercles arranged in a circle around the genital pore, higher than the area of plate next to the periproct. The whole plate is lightly sculptured. The madreporic part of genital plate 2 covers most of the plate, and usually obscures the position of the genital pore by its perforations. On genital plate 5, two low, rounded ridges extend from the anterior limb of the 'boomerang' (see p. 65) to meet the raised rim around the genital pore. On the lectotype there are several thin striations extending from the plate margins next to the interambulacra towards the periproct; they are parallel with the anteroposterior axis on the adoral margin close to the interradius, and nearly parallel away from the interradius.

3) Periproct. The shape is approximately that of an elongated pentagon, with three shorter sides formed by the anterior parts of the periproctal margins of genital plates 1 and 4, and by all of the periproctal margins of genital plates 2 and 3. The two larger sides are formed by the posterior parts of the periproctal margins of genital plates 1 and 4, by all of the periproctal

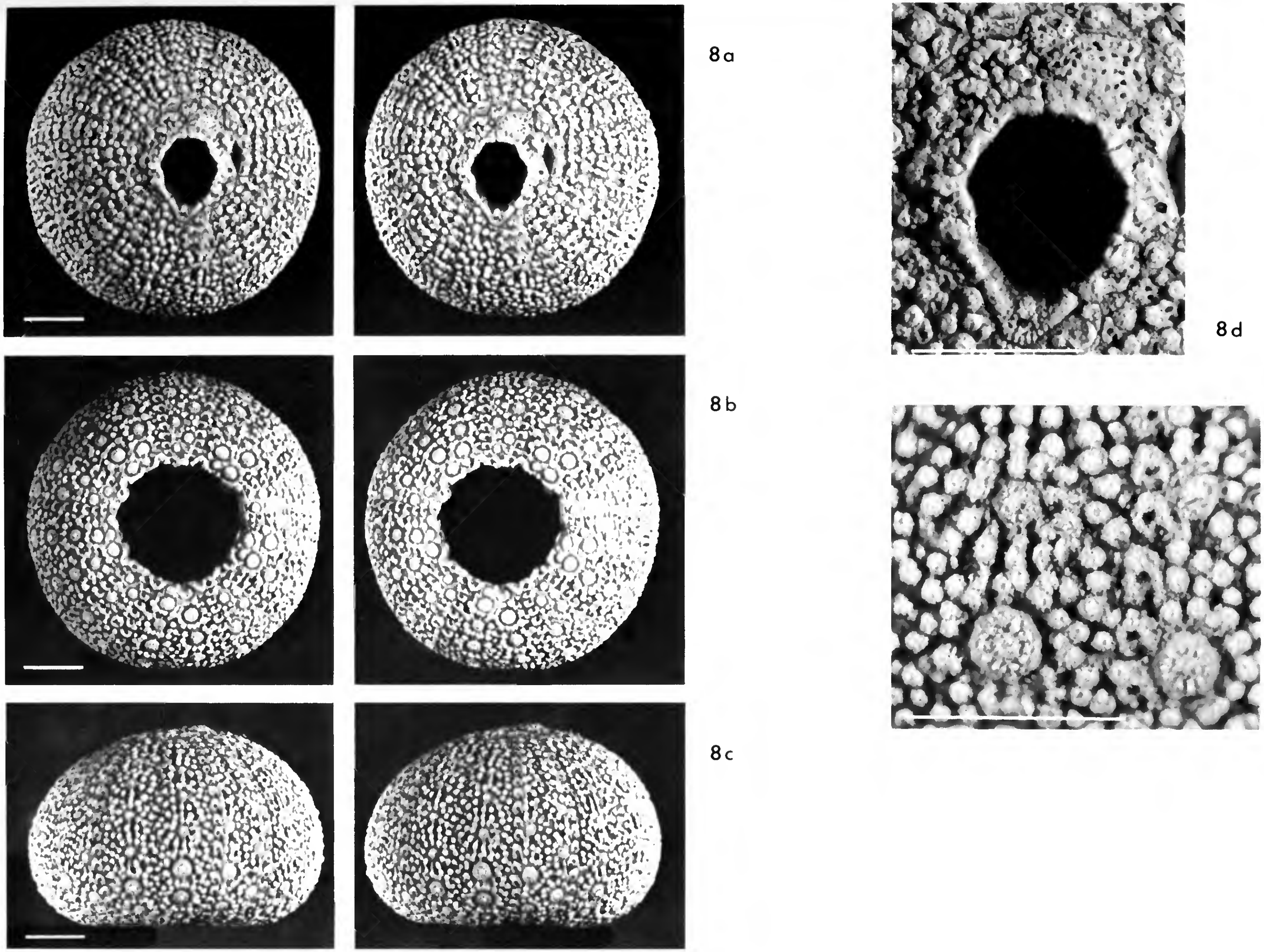


Fig. 8 *Boletechinus rowei rowei* (Gregory), **lectotype** E39372, herein selected. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), apical disc; (e), interambulacral ornament at the abrupt increase in size of tubercles, and part of an adjacent ambulacrum. Scale bars 1 mm.

margins of genital plate 5, and by ocular plates I and V. The periproct is about 25% longer than wide.

Ambulacra. The ratios of the width of the ambulacra to the width of the interambulacra in the lectotype are: at the apical disc 1 : 1·6; at the ambitus 1 : 1·5; at the peristome 1 : 1·25. On the simple plates, the secondary tubercles occur singly at the perradial edge of the plate and also on the adapical adradial part of the plate, close to the pore-pairs of both simple and compound plates. The arrangement of the secondary tubercles together with the primary tubercles, and the shallow sculpturing, gives the appearance of two ribs per ambulacrum, extending from the apical disc to a position just adoral to the ambitus. The lack of sculpturing along the plate margins gives a uniform appearance to the ambulacra, with the individual plates indistinct.

Interambulacra (Fig. 8e). At the ambitus and adorally two secondary tubercles coalesce to form a ridge which extends from the adoral edge of a primary boss to two secondary tubercles of the next scrobicular circle. The other two tubercles are also in contact with the boss of the primary tubercle. Adapical to the ambitus there are up to four secondary tubercles extending from the adoral part of one primary boss to the adapical part of the next adoral primary boss. The effect of this arrangement is to produce two thin, discontinuous ribs along each column of interambulacral plates. Other secondary tubercles are situated quite close to each other and form rows which radiate from the primary tubercle to give a stellate appearance to the plate. Between all the secondary tubercles the test is lightly excavated to produce the spoked effect on the scrobicules. Lack of sculpturing along plate margins gives a uniform appearance to the ornament, with the boundaries of the individual plates indistinct.

Peristome (Fig. 8b). The auricles are short, angular and peg-like.

Boletechinus rowei (Gregory) ***anglicus*** subsp. nov.

Figs 2a, 3a–f, 9a–e, 10

1900 *Zeuglopleurus rowei* Gregory: 353–354, fig. 4.
1943 *Zeuglopleurus rowei* Gregory; Mortensen: 352–353.

Diagnosis. A *Boletechinus* with plate margins well defined by sculpturing; secondary tubercles close together and confined within excavated areas; deep sculpturing between secondary tubercles; distinct excavated area usually present along the interradius, tapering adorally from apical disc to ambitus.

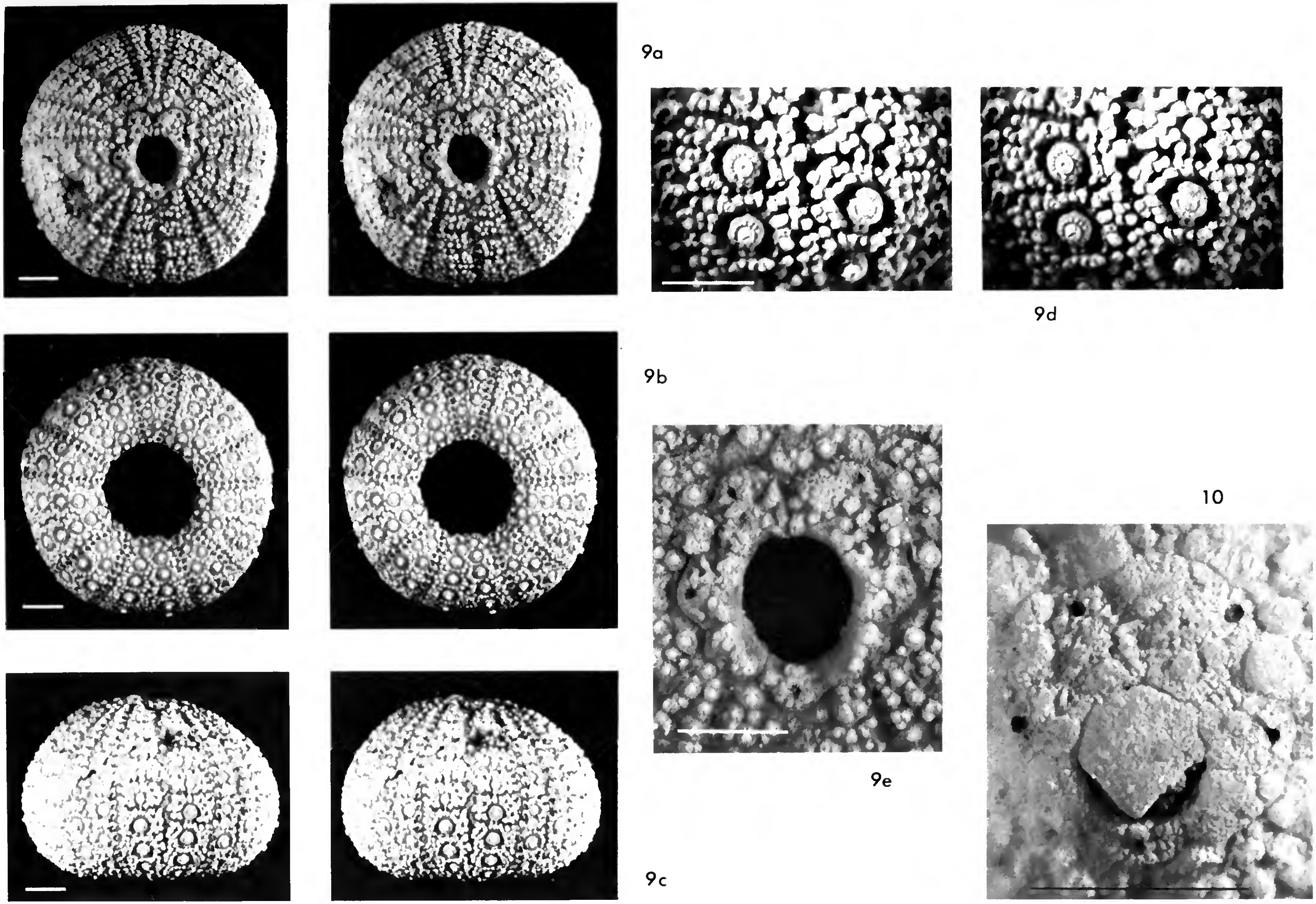
Holotype. BM(NH) 75556a (Fig. 9), a syntype of *Zeuglopleurus rowei* Gregory, from the Senonian of Charlton, Kent.

Paratypes. BM(NH) 75556b, a syntype of *Zeuglopleurus rowei* Gregory, from the Senonian of Charlton, Kent; E39377–8 from the Santonian, base of *Marsupites* band, Thanet Coast, Kent; E39373 from the Santonian, base of the *Uintacrinus* band, Thanet Coast, Kent; E39805 from the same horizon at Flamborough Head, Yorkshire; E39376 from the Santonian, *Uintacrinus* band, Thanet Coast, Kent; GSM 118257 (Fig. 10) and 118258 from the Santonian, *coranguinum* Zone, 4·5 m above Whitaker's 3-inch band, Kingsgate, Thanet, Kent; GSM 118259 from the Santonian, *coranguinum* Zone, 0–0·5 m above Bedwell's Columnar Band, West Ramsgate, Thanet, Kent. All GSM specimens are from the A. S. Gale collection.

Preservation. The specimens are all well preserved except for E39378 and E39376, which have been broken so that only parts of the tests remain.

Shape (Figs 3a–f). The dimensions of the holotype are: diameter of test 8·0 mm; height of test 5·6 mm; diameter of peristome 3·0 mm.

The holotype is a particularly large and fine specimen; a specimen of average size, such as E39377, has the following measurements: diameter of test 4·4 mm; height of test 2·9 mm; diameter of peristome 2·0 mm.



Figs 9–10 *Boletechinus rowei anglicus* subsp. nov. Fig. 9, **holotype** 75556a. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), stereo photograph of part of the interambulacral ornament; (e), apical disc. Fig. 10, GSM 118257. Apical disc of a small paratype, showing the periproctal plate in position. Scale bars 1 mm.

APICAL SYSTEM. 1) Ocular plates. The ornament consists of several tubercles developed close together, forming on oculars II–IV an approximately rectangular portion raised sharply above the general level of the plates. A raised part of oculars I and V forms an elongate ridge with three large tubercles. Each plate is strongly sculptured around the tubercles and margins.

2) Genital plates and madreporite. The ornament consists of small tubercles and swellings above the general level of the plates, and deep excavations between adjacent apical plates and between tubercles. On the holotype, along the margins between adjacent genital plates 2–4, the excavations are deeper than they are between genital plates 1 and 4 and oculars I and V. There are no excavations between genital plate 5 and oculars I and V. The genital pore of plate 2 is recognizable, and is usually situated on a low, more or less triangular-shaped portion of the plate, near the interradial suture.

3) Periproct. The periproct has a scalloped appearance where the ornament of the component plates bulges into it. The periproct is about 15% longer than wide. The well-defined, raised ornament of all the component plates, except genital plate 5, forms a rim around the periproct. The lower ornament of plate 5 makes it almost level with the general surface of the test.

A single specimen (GSM 118257, Fig. 10) has preserved *in situ* a large, single anal plate which covers almost all of the periproct except for two small openings at ocular plates I and V. The plate fits closely to the periproctal margins of genital plates 1–4, but at the anterior ends of ocular plates I and V the margins of the anal plate are straight and extend directly to interradius 5 where they join at a point. Here the plate is not in close contact with genital plate 5. The two openings either side of the anal plate and periproctal margin are not the same size; the opening by ocular I is twice the size of the opening by ocular V. No other anal plates are preserved within the opening, so it is likely that the anus was protected by tiny plates on the anal integument.

AMBULACRA. The ratios of the width of the ambulacra to the width of the interambulacra of the holotype are: at the apical disc 1 : 2·5; at the ambitus 1 : 1·7; at the peristome 1 : 1·4. The holotype 75556a and paratype 75556b have both perforate and imperforate mamelons on the primary tubercles. Imperforate mamelons occur adapical to the ambitus; perforate mamelons occur at the ambitus and adorally, but only on the compound (diad) plates. In other respects the characters are those of *Boletechinus* type. Sculpturing of plates occurs along the perradial margins of all plates, along the transverse margins of simple adapical plates, and around the individual secondary tubercles of the compound plates. Perradial excavations taper adorally and are absent on the oral surface. The horizontal sutures of the oral surface are not sculptured. The sculpturing around plate boundaries makes the outline of the individual plates distinct.

INTERAMBULACRA. The holotype, and paratype 75556b, have perforate mamelons from the ambitus adorally. Secondary tubercles form contiguous scrobicular circles and up to three other incomplete circles with occasional extra tubercles along the perradial margin of the plate. The scrobicular area is well defined on larger primary tubercles because the secondary tubercles are further from the primary boss than they are on smaller primary tubercles. The sculpturing of the interambulacra is present along the horizontal margins of plates adapical to the ambitus, where it follows the outline of the secondary tubercles. Distinct sculpturing also occurs along the interradial margins, again following the outline of the tubercles. This sculpturing is a wide excavation adapically and tapers to a very thin excavation near the peristome (Fig. 9d). However, the excavation of the interradial area is not well developed in all specimens.

The horizontal sutures are also 'divided' by a single or by two short, low, radiating ridges which extend from an adapical primary boss to the adoral scrobicular tubercles. These ridges are best developed at the ambitus adapically. From the ambitus adorally, ridges are less well developed and contiguous scrobicular tubercles only occur, to separate one plate from the next. Sculpturing between adapical plates and adoral plates from the ambitus adorally becomes less distinct, until it is hardly present at all on the oral surface. The sculpturing along the adradial suture follows the outline of the secondary tubercles and the tilted part of adjacent ambulacral plates, to give a notched appearance.

PERISTOME. The auricles are short, broad, leaf-shaped prongs with a 'keyhole'-shaped space between the prongs of a pair.

NOTES ON THE PERFORATION OF THE TUBERCLES. Although the primary tubercles of the holotype 75556a and the paratype 75556b, from ambitus adorally, are perforate, the perforations are quite small and were overlooked by Gregory (1900). None of the other specimens of either *B. r. rowei* or *B. r. anglicus*, nor any of the American specimens, have perforate tubercles. Perforations in the primary tubercles of *Tylocidaris* can be found in the most adapical interambulacral plates, which show a secondary loss of perforation (see Lewis & Ensom 1982: 102), but the retention in *B. r. anglicus* of perforations from the oral surface to the ambitus in specimens of greatly differing sizes—75556a is 8 mm in diameter, 75556b is 4·2 mm in diameter—is puzzling.

Genus *ZEUGLOPLEURUS* Gregory 1889

TYPE SPECIES. *Zeuglopleurus costulatus* Gregory 1889.

DESCRIPTION[1]. *Shape*: A small regular echinoid with an approximately hemispherical test, with the anterior end slightly higher than the posterior end.

Apical System: 1) Ocular plates. Ocular plates I and V are insert. All the oculars have M-shaped margins next to their ambulacra. The ornament consists of tubercles and excavations.

2) Genital plates and madreporite. These form the anterior, lateral and posterior-most margins of the periproct. Genital plate 5 is smaller than the other four genital plates, has no distinct swelling into the periproct, and has a central pore. The other genital pores are slightly perradial in position, towards the anterior paired ambulacra. The madreporite is slightly raised and has many small pores. The ornament of the plates consists of small tubercles, granules and excavations, except for plate 5 which has no ornament.

3) Periproct. The boundary composed of ocular plates I and V and genital plates 1–4 may be raised as a rim, whilst the boundary composed of genital plate 5 remains flush with the test. The periproct is slightly elongated anteroposteriorly.

Ambulacra: These are straight, and taper adapically and adorally and are widest at the ambitus. The pore-pairs are arranged in monoserial columns and are oblique, with the adradial pore more adapical than the perradial pore. The first few plates from the apical disc adorally are simple; they then become compounded in the acrosaleniid manner. The ornament consists of primary and secondary tubercles and sculpturing and excavation of the test.

The primary tubercles each have a low, convex, crenulated boss, and a large, imperforate hemispherical mamelon with an undercut neck. Scrobicules are also present.

Secondary tubercles have low, convex bosses and small hemispherical mamelons. They form scrobicular circles and occupy other areas of the plates.

Sculpturing consists of excavations along sutures and around secondary tubercles, and is best represented adapically to the ambitus. Adorally from the ambitus the sculpturing is reduced.

Interambulacra: These taper adorally and adapically and are widest at the ambitus. The ornament is similar to that of the ambulacra. The tubercles of both interambulacra and ambulacra increase in size steadily to the ambitus, then decrease steadily.

Peristome: This is decagonal and is slightly elongated anteroposteriorly. The gill-slits are shallow.

RANGE. Upper Cretaceous of Europe.

Zeuglopleurus costulatus Gregory
Figs 2a, 3a–f, 11a–e

1889 *Zeuglopleurus costulatus* Gregory: 495–496, figs 1–5.
1889 *Zeuglopleurus costulatus* Gregory; Duncan: 103.
1911 *Zeuglopleurus costulatus* Gregory; Lambert & Thiéry: 217.

[1] See also the diagnosis by Gregory, 1889.

1935 *Zeuglopleurus costulatus* Gregory; Lambert & Jeannet: 6.
1943 *Zeuglopleurus costulatus* Gregory; Mortensen: 352–353, text-figs 211a–d, 212, 213.

DIAGNOSIS. Test slightly flattened posteriorly; apical disc fairly large; periproct slightly elongate and slightly posterior; peristome of moderate size, slightly elongated anteroposteriorly; ornament includes deep excavations and adapical–adoral ridges connecting adjacent plates and radiating ridges on scrobicules.

HOLOTYPE. BM(NH) E4365 (Fig. 11), from the Cenomanian, Chalk Marl, *varians* Zone, of Glynde, near Lewes, Sussex. All measurements referred to in the description are those of the holotype.

OTHER MATERIAL. E39790–3, E79244, from the Turonian, *cuvieri* Zone from the south Devon coast. All the material is in the collections of the BM(NH), Department of Palaeontology.

PRESERVATION. The type specimen is well preserved, uncrushed and has most of its tubercles intact except for those of the oral surface. These are slightly abraded. The specimens from Devon have all lost their ocular and genital plates; one specimen—E39792—is crushed, and others of the group have incomplete tests.

SHAPE. The holotype is approximately hemispherical, with the anterior end slightly higher than the posterior end. The peristome is elongated anteroposteriorly and is of moderate size. The periproct has the outline of an inverted comma, and has a raised rim except at genital plate 5.

Table 4 Dimensions (mm) of the holotype E4365 of *Zeuglopleurus costulatus* Gregory.

	Diameter of test	Height of test	Diameter of peristome	Diameter of apical disc
Post.-Ant.	11·0	6	4·4	5·0 (III–5)
Lateral	10·75		3·8	4·0 (4–1)

APICAL SYSTEM (Fig. 11d). 1) Ocular plates. Ocular plates I and V are about 25% longer than oculars II, III and IV, and all have irregular outlines and concave periproctal margins. Oculars II, III and IV all have six sides.

The ornament of all the oculars consists of many small tubercles very close together, giving a swollen appearance to the plates. Oculars I and V have a wide, smooth rim adjacent to the periproct. At each M-shaped margin the plate is deeply excavated, and has a tiny, diamond-shaped area with minute granules on the surface. The ocular pore is obscured.

2) Genital plates and madreporite. Genital plates 1, 2, 3 and 4 form the anterior and lateral margins of the periproct. The periproctal margins of plates 2, 3 and 4 are gently concave; that of plate 1 has a convex bulge along the anterior two-thirds and extends downwards and obliquely to the vertical margin of genital plate 2 (see Fig. 11d). The bulge may possibly be a single periproctal plate which has remained in position *post mortem*, but the suture between it and the rest of plate 1 cannot be seen. It is this bulge which gives the periproct its comma shape. The periproctal margins of plates 1 and 4 are about twice as long as those of 2 and 3.

Genital plate 5 is considerably smaller than the others and forms part of the posterior rim of the periproct.

The ornament of the genital plates consists of very small tubercles and granules randomly distributed over the surface. In between the tubercles there are deep, circular or elongated excavations, except between the tubercles of plate 5. The madreporite has an approximately circular outline, and with many small perforations over the surface. The genital pore of plates 3 and 5 is interradial in position. The pore is situated near the adoral side of plates 1–4, and centrally in plate 5, and is slightly elongated in the direction of the interradius.

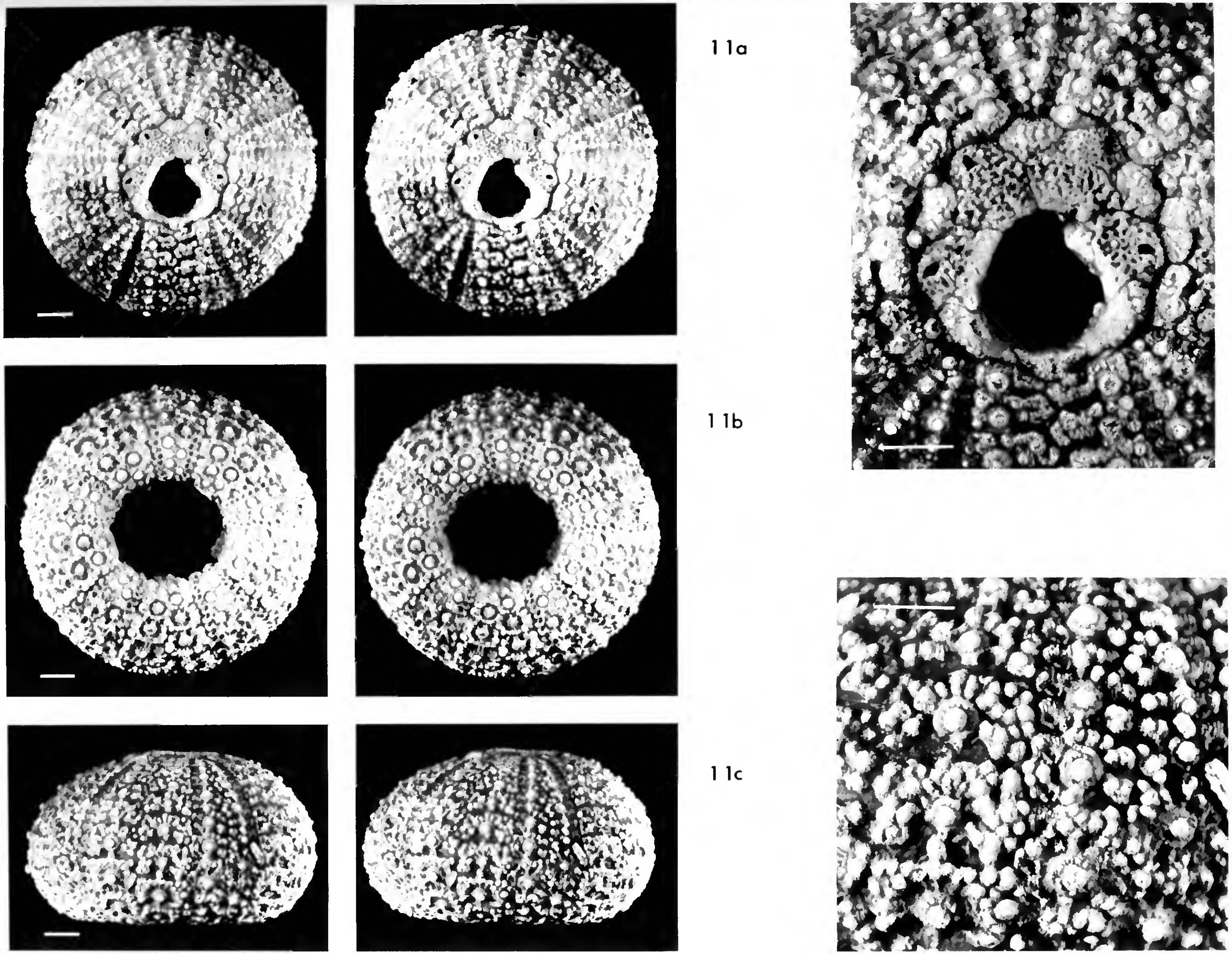


Fig. 11 *Zeuglopleurus costulatus* Gregory, holotype E4365. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), apical disc; (e), ambulacral and interambulacral ornament. Scale bars 1 mm.

The periproctal margins of genital plates 2, 3 and 4 are angular, whilst those of plates 1 and 5 are rounded, with the smooth inner surface of the periproctal margin extending for a short distance over the outer edge of the plates.

Table 5 Dimensions of genital plates in holotype of *Zeuglopleurus costulatus* Gregory. L = maximum length between adradial margins; W = maximum width, periproctal margin to interradial suture (mm).

Plate	L	W
1	1·2	1·2
2	1·35	1·3
3	1·2	1·25
4	1·15	1·1
5	1·05	0·5

3) Periproct. The outline of the periproct is comma-shaped, possibly because of an included periproctal plate. The longest dimension along the anteroposterior axis is about 2·2 mm, and the widest part of the 'comma' measures about 2·0 mm. The periproctal border is smooth and has no ornament on genital plates 1, 4 and 5 and oculars I and V. The ornament of genital plates 2 and 3 extends to the periproct. The border is raised as a rim above the general level of the test, slightly lower at the anterior end and much lower at the posterior end. The adradial ends of oculars I and V and all of genital plate 5 are at the same lower level.

AMBULACRA (Fig. 11e). These are straight, taper adorally, adapically, and are widest at the ambitus. The ratios of the width of the ambulacra to the width of the interambulacra are:

at the apical disc 1 : 3·3
at the ambitus 1 : 1·5
at the peristome 1 : 1·3

The simple plates are the two to five most adapical plates, followed by compound plates of acrosaleniid type. There are some diads adapical to the ambitus which are present between acrosaleniid compound plates.

Table 6 Number of plates in each ambulacral column in holotype of *Zeuglopleurus costulatus* Gregory.

	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	Va	Vb
Simple	2	3	5	4	2	3	2	2	2	4
Diads	4	1	1	0	2	2	4	3	0	0
Triads	5	7	7	8	8	7	6	7	9	8

The pore pairs are small, oblique and very slightly elongated, with the long axis of the adradial pore parallel to the transverse sutures and the long axis of the perradial pore adapical–perradial adradial–adoral. The pores are slightly sunken into a lobed part of the plate, with the margin of the perradial pore open at a narrow gap on the adoral side. The pores are situated in the adoral perradial 'corner' of the lobe, and are separated from each other by a fairly wide wall.

The ornament of the ambulacra consists of large primary tubercles, small secondary tubercles and tiny ridge-like and teardrop-shaped granulations, and deep excavations along sutures and around tubercles.

Each primary tubercle has up to about thirteen small crenulations. Scrobicules are present on the compound plates, narrow on the diads and wide on the others. The wide scrobicules have eight or nine thick radiating ridges extending radially from the primary boss to the scrobicular tubercles.

The ridge and teardrop granulations are very small—a typical teardrop is 0·1 mm long, a ridge is 0·14 mm long. Their long axes are parallel to the perradius; the ridges are arranged side-by-side, while the teardrops alternate with each other and interlock.

The primary tubercles form two columns in each ambulacrum. The simple plates have a tubercle in the centre, the diad compound plates have the adoral tubercle overlapping the adapical plate, the acrosaleniid compound plates have the large tubercle in the centre of the two adapical plates and the third simple plate has a very small primary tubercle of the same size as the secondary tubercles.

The secondary tubercles form incomplete scrobicular circles and are present on all plates except the most adapical ones. The adapical diad compound plates have only one or two along the perradial part of the plate, but those nearer to the ambitus have more secondary tubercles, up to four of them, along the perradial margin. The acrosaleniid compound plates have secondary tubercles along the adapical edge, perradial edge and adoral edge of the plate. The simple plate between adjacent compound plates shares its secondary tubercles so that there is a 'clumping' of tubercles between the compound plates. There is usually a single secondary tubercle, *or* a scrobicular ridge, between adjacent adoral and adapical plates, which is in close contact with the boss and which together with the primary tubercle forms two discontinuous but prominent ridges down each ambulacrum from the apical disc to the ambitus. From the ambitus adorally the ridges are insignificant. On the oral surface the scrobicules become much narrower, concomitant with the reduction in size of the plates, and the ornament is simplified.

On a few compound plates a single tubercle occurs on the adradial adapical part of the lobe which bears the pore pair.

The granulations are best developed on the adapical side of the lobe of the pore-pairs, but less developed ones are also present on the secondary tubercles along the perradial sutures. The deep sculpturing is mostly confined to the area of the test between apical disc and ambitus, and is represented by deep excavations along sutures and around secondary tubercles. The secondary tubercles are undercut on the adapical edges of the plate. Adoral to the ambitus the excavations are much reduced and are very weak along the adradial sutures.

INTERAMBULACRA (Fig. 11e). The ratios of the width of an interambulacrum at the peristome, the ambitus and the apical disc are: 1·5 : 2·5 : 1.

The ornament is similar to that of the ambulacra. Each primary tubercle has a small convex boss which is elongated at its adoral side into a single or forked ridge. The boss has about fifteen small crenulations and a very narrow platform.

The primary tubercles are situated in the middle of the plates, and secondary tubercles are present on the adapical, adradial and interradial parts of each plate, but not on the adoral parts. The secondary tubercles form approximately semicircular scrobicular arcs around the primary tubercles—slightly less than semicircular nearer the apical disc to slightly more than semicircular at the ambitus and adorally. There are also up to two additional arcs of secondary tubercles present on the adradial and interradial margins of the plates, except on plates immediately next to the peristome where only one semicircle of tubercles is present. There are thick ridges extending radially from the base of the primary boss to adjacent secondary tubercles. On plates at the ambitus and adoral to it, the secondary tubercles are raised to the same level as the primary mamelon. On the adoral edge of the plate there is one thick ridge from the primary boss to the adapical scrobicular semicircle of the adjacent adoral plate. This ridge is very thick adapically, but adorally, towards the ambitus and adoral to the ambitus, the ridge bifurcates into a narrow, inverted V-shape. These ridges, together with the primary tubercles, give an appearance of two discontinuous ribs down the interambulacrum to the oral surface, where they cease.

The granulations are similar to the ridge type found on the ambulacra, but are much less

pronounced and less extensive. They are present at the adradial and interradial sides of the plates. The sculpturing is very wide and fairly deep, and slightly undercuts the adapical edges of the scrobicular semicircles. The excavations are approximately triangular areas either side of the thickened and bifurcated ridges. Other excavations are present around the secondary tubercles along interradial and adradial margins. The sculpturing and excavations are much reduced or absent on the oral surface.

There are between 10 and 12 plates in each interambulacral column.

PERISTOME (Fig. 11b). This is slightly elongated anteroposteriorly, and has shallow but distinct gill slits. The gill slits have a narrow rim which is continuous from one slit, across the oral extremity of the interambulacrum to the other slit. The inside of the test of the holotype has some matrix remaining, and a small calcareous overgrowth which has extended into the peristome. However, the apophyses are visible as low, robust structures, and the auricles of Ia, Ib, IIa, IIIa, IIIb, IVa, IVb, Vb are also present, forming short peg-like structures, unjoined in the middle.

Comparisons between *Boletechinus*, *Zeuglopleurus*, and other genera

Boletechinus delawaricus differs from *B. mcglameryae* in its ornament, in the less abrupt increase in size of its primary tubercles, and in the shape of the genital plates. The ornament of *B. delawaricus* has a less granular appearance than that of *B. mcglameryae*; the ridges enclosing the diamond-shaped depressions between adjacent interambulacral plates of *B. delawaricus* are represented in *B. mcglameryae* by two almost parallel ridges. Genital plate 5 of *B. mcglameryae* is elongated adorally almost to a sharp point, with the narrow width accentuating the point, whereas in *B. delawaricus* the plate is not elongated into a point; the width is much greater than the length, so that the sharp point is not produced. The apical disc of *B. delawaricus* is more elongate and has an oval outline whilst that of *B. mcglameryae* is angular. The diameter of the peristome of *B. delawaricus* is between 42% and 44% of the diameter of the test (mean 43%), whilst the diameter of the peristome of *B. mcglameryae* is between 33% and 41% of the diameter of the test (mean 37%; Cooke (1955) says '. . . nearly one third . . .'): see Fig. 3e, p. 67.

Boletechinus r. rowei differs from *B. mcglameryae* by having a stellate arrangement of secondary tubercles on the interambulacral plates. The plate boundaries of *B. r. rowei* are much less well defined than are those of *B. delawaricus*. The most obvious difference between the two subspecies of *B. rowei* is the much stronger sculpturing present on *B. r. anglicus*, especially around the plate margins. The boundaries of the plates of *B. r. anglicus* are quite distinct, whereas those of *B. r. rowei* are indistinct, giving the test a much more uniform appearance in its tuberculation. The interradial excavation on many specimens of *B. r. anglicus* assists further in their distinction. In other respects the two subspecies are difficult to separate. The sculpturing of the test of *B. r. anglicus* is very similar to that of *Z. costulatus*, so that Gregory (1889) regarded specimens 75556a and b—the holotype and a paratype of *B. r. anglicus*—as juveniles of *Zeuglopleurus costulatus* in his original descriptions. He later changed his mind and in 1900 placed these supposed 'juveniles' with *Z. rowei*. However, the abrupt increase in the size of the primary tubercles at the ambitus of the *Boletechinus* easily distinguishes *B. r. anglicus* from *Z. costulatus*.

Glyptocyphus difficilis may be distinguished from *Zeuglopleurus costulatus* by having irregularly developed ambulacral plate-compounding. *G. difficilis* frequently has groups of compound ambulacral plates which have no enlarged primary tubercles. The compounding is acrosaleniid but is also irregularly developed. *Z. costulatus* has a more regularly developed acrosaleniid compounding.

Echinocyphus tenuistriatus differs from *Z. costulatus* in its different ornament, which consists of a broad inverted V-shaped excavation along the adoral edge of the plates. The secondary tubercles are smaller and more widely separated than those of *Z. costulatus*. Although the difference between these two species is evident, *Echinocyphus* and *Zeuglopleurus* may yet prove to be congeneric; however, the discussion of this lies outside the scope of the present paper.

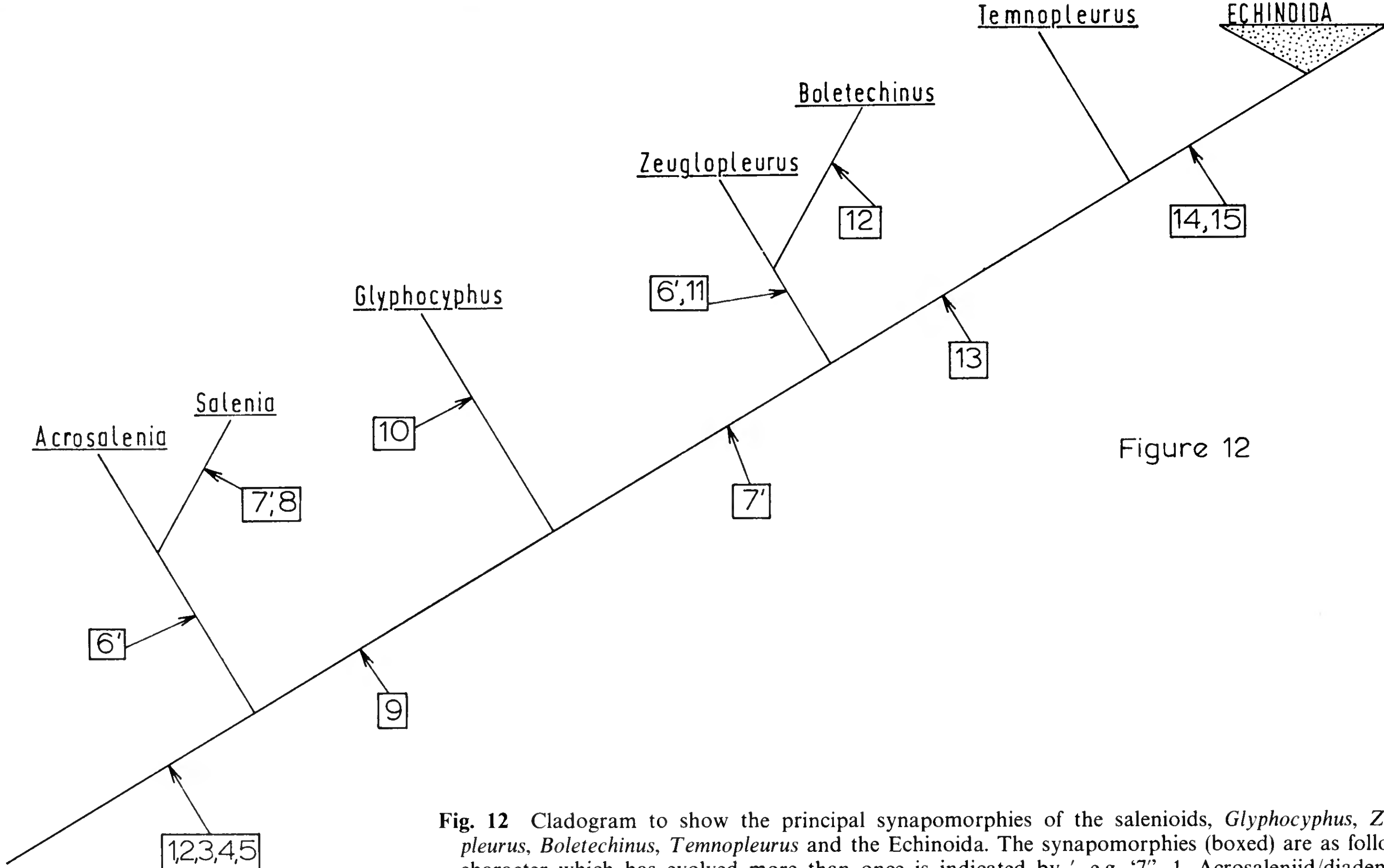


Fig. 12 Cladogram to show the principal synapomorphies of the salenioids, *Glyphocyphus*, *Zeuglopleurus*, *Boletechinus*, *Temnopleurus* and the Echinoida. The synapomorphies (boxed) are as follows; a character which has evolved more than once is indicated by ′, e.g. '7′'. 1, Acrosaleniid/diadematoid compounding; 2, Perforate tubercles; 3, Crenulate tubercles; 4, Tubercle size increase gradual to ambitus, no abrupt increase; 5, Dicyclic disc; 6, Large suranal plate(s) retained in adults; 7, Tubercles imperforate; 8, Single suranal plate tessellated into disc; 9, Sculptured test; 10, Monocyclic disc; 11, Oculars I and V insert; 12, Abrupt increase in size of tubercles at ambitus; 13, Echinoid compounding; 14, Loss of test sculpturing; 15, Loss of tubercle crenulation.

Species of *Zeuglopleurus* other than *Z. costulatus* are recorded from Europe, and include *Z. colleti* (Turonian of France) which has straight pore-pairs, and sculpturing of the horizontal sutures similar to those of *Z. costulatus* but elsewhere not so extensive. Mortensen (1943: 353) reported that a specimen he examined by grinding down the test showed '. . . the echinoid type of ambulacra . . .', unlike the acrosaleniid type of *Z. costulatus.*

Z. glanoviensis Kongiel 1939 (Turonian of Poland) is flattened adorally and adapically, and has unigeminate ambulacra with compound plates '. . . almost unfused . . .'.

Z. pusillus (Roemer 1840) (Cretaceous of Germany) has a flattened oral surface and a circular periproct, but other details of structure and ornament cannot be seen in the figures of Roemer, and his descriptions are inadequate.

Z. (?) *cannabis* (Desor 1858) is imperfectly known as Desor did not give a figure. Gregory (1889) regarded it as probably a *Zeuglopleurus*, differing from *Z. costulatus* in that '. . . the tubercles are less conjugate; the apical system is also less annular . . .'.

Stratigraphical distribution of *Boletechinus* and *Zeuglopleurus*

Stratigraphical details supplied with the specimens in the Rowe collection, BM(NH) and with specimens in the collections of A. S. Gale, GSM, show that the two species of *Boletechinus* from England are at present confined to the Santonian and Campanian. The majority of specimens of *B. r. rowei* in the Gale collections come from around Bedwell's Columnar Band, *Micraster coranguinum* Zone, and two others from the middle *Uintacrinus* Zone of the Santonian. Specimens of *B. r. rowei* in the Rowe collections are recorded from the *quadratus* Zone of the Campanian and the *Marsupites* and *Uintacrinus* Zones of the Santonian.

Specimens of *B. r. anglicus* in the Gale collections come from Whitaker's 3-inch band, *M. coranguinum* Zone, and from about 0·5 m above Bedwell's Columnar Band (see Rowe 1900: 289–367). Specimens in the Rowe collections come from the *Marsupites* and *Uintacrinus* Zones.

The two American species of *Boletechinus* are from the Maastrichtian.

Table 7 Summary of distribution of *Boletechinus* and *Zeuglopleurus* species.

			Senonian					
				Santonian				
	Cenomanian	Turonian	Coniacian	*coranguinum* Zone	*Uintacrinus* Zone	*Marsupites* Zone	Campanian	Maastrichtian
B. mcglameryae	–	–	–	–	–	–	–	X
B. delawaricus	–	–	–	–	–	–	–	X
B. r. rowei	–	–	–	X	X	X	X	–
B. r. anglicus	–	–	–	X	X	X	–	–
Z. colleti	–	X	–	–	–	–	–	–
Z. glanoviensis	–	X	–	–	–	–	–	–
Z. costulatus	X	X	–	–	–	–	–	–

Species of *Zeuglopleurus* are known from the Cenomanian and Turonian. *Z. costulatus* comes from the *varians* Zone of the Cenomanian and the *cuvieri* Zone of the Turonian, and *Z. colleti* and *Z. glanoviensis* are said in their descriptions to come from the Turonian. Age details of other species of *Zeuglopleurus* are not given in their descriptions.

Acknowledgements

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Index

New taxonomic names and the page numbers of the principal references are on **bold** type. An asterisk (*) denotes a figure.

Accepted for publication 16 April 1985

British Museum (Natural History)

Catalogue of the type and figured specimens of fossil Echinoidea in the British Museum (Natural History)

David N. Lewis

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The trilobite fauna of the Raheen Formation (upper Caradoc), Co. Waterford, Ireland

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Contents

Synopsis

The Raheen Formation contains a diverse trilobite fauna dominated by *Tretaspis ceryx* Lamont and *Ampyx austinii* Portlock, which are redescribed along with *Homalopteon portlockii* (Salter) and *Salteria involuta* Salter. Ten other species are described, including *Sphaerocoryphe murphyi* sp. nov. and possible new species of *Mesotaphraspis* and *Flexicalymene*. A lectotype of *Homalopteon portlockii* (Salter) is selected, and a neotype designated for *Ampyx austinii* Portlock. The fauna is thought to represent a fairly deep water assemblage of late Caradoc age.

Introduction

The Ordovician sedimentary and volcanic rocks north of Newtown Head, Co. Waterford (S 700070, Fig. 1) were first discussed in detail by Reed (1899: 721–725), although elements of the fauna had previously been described by Portlock (1843), M'Coy (1846), Salter (1849, 1864) and Davidson (1866). Reed (1899: fig. 1) introduced the term 'Raheen Shales' for the fossiliferous sandy mudstones and provided a faunal list based on his own and earlier collections.

Bull. Br. Mus. nat. Hist (Geol.) **40** (3): 91–122

Issued 26 June 1986

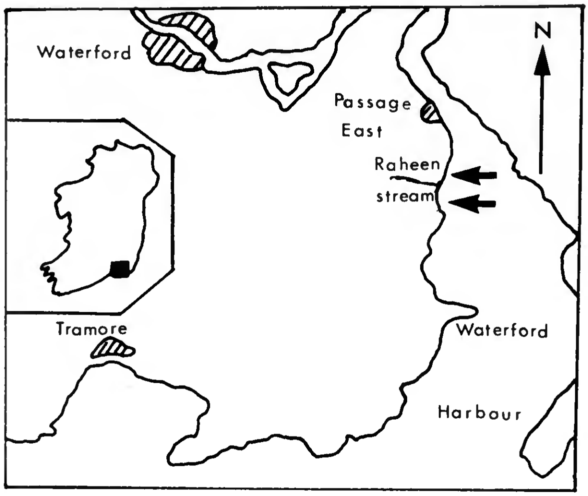


Fig. 1 Map showing localities (arrowed) of Raheen Formation exposures along west bank of Waterford Harbour.

Since then, the unit has received little published attention although Mr G. J. Murphy studied the formation in the 1950s in conjunction with his work on the older Tramore Limestone. The Ordovician stratigraphy of Co. Waterford has been formalized in recent years (Mitchell *et al.* 1972, Williams *in* Williams *et al.* 1972, Carlisle 1979), with the sequence at Newtown Head largely being ascribed to the Raheen Group of which the Raheen Shale Formation forms a part. A simplified section through the formation was given by Paul (1984: fig. 42).

Several trilobite species have been described originally from the Raheen Formation (Portlock 1843, Salter 1849, 1864, Lamont 1941). One of these, *Homalopteon portlockii* (Salter), is the type species of its genus. The present study involves the redescription of these as well as the other trilobites, a quantitative assessment of the trilobite fauna and a consideration of the age of the formation.

Sampling

The foreshore sequences north and south of the Raheen Stream were examined and sampled by Tripp and Morris in 1981 and 1982. The succession north of the stream is heavily tectonized and probably includes older strata (possibly the late Llandeilo–early Caradoc Tramore Limestone) which are poorly fossiliferous but yielded specimens of *Ampyxina*, a taxon not represented in the Raheen Formation. The strata above these beds on the north side of the stream include a typical Raheen fauna and are included in the descriptions herein (Sample N, Table 2, p. 94). The more complete sequence south of the stream dips steeply to the north-west and limited sedimentary evidence suggests it may be inverted. The section was measured and ten large samples made (see p. 93). Blocks containing fossils were collected and in many cases were broken up further in the laboratory, prior to and during examination under the binocular microscope. The new type and figured specimens along with a representative sample of each species are now housed in the Department of Palaeontology, British Museum (Natural History), London (numbers prefixed It); the remainder have been donated to the National Museum of Ireland, Dublin. The majority of the trilobites recovered (551 out of 719) were from Sample 3, which comprises two collections of approximately equal numbers made on each of the two sampling seasons. They proved to be virtually identical in percentage composition, indicating the thoroughness of the sampling. The sample horizons and general lithologies are shown in Table 1.

Table 1 Sample horizons and general lithologies of sequence south of Raheen stream, Co. Waterford. Note that many of the beds are ashy, and the overall abundance of ash increases up the succession.

Sample	Thickness	Lithology
[TOP]		thick felsite intrusion
10	2·3 m	olive brown shales
	[1·5 m	no exposure]
9	2·9 m	olive green/brownish shales with nodules
8	2·8 m	massive dark ashy mudstones
7	5·5 m	olive green/brownish shales with nodules
6	4·0 m	soft shales
5	1·1 m	olive green/brownish shales with nodules, extensively faulted thin (1 cm) chert band
4	6·1 m	grey/green mudstones
3	1·8 m	dark grey/green mudstones with nodules
	2·9 m	felsite intrusion
2	1·8 m	dark grey rusty-weathering shales
	1·0 m	felsite intrusion
1	2·8 m	light grey rusty-weathering shales
[BASE]		
	Total 36·5 m	

Fauna

The fauna of the Raheen Formation is dominated by trilobites and brachiopods, but rarer elements include echinoderms (see Paul 1984), bryozoans, gastropods, machaeridians, ostracods and graptolites. The brachiopod fauna is being assessed by Dr D. A. T. Harper of University College, Galway but the dominance of *Onniella* noted by Reed (1899: 723, as '*Orthis argentea*') is confirmed (personal communication D. A. T. Harper, August 1984). The composition of the trilobite fauna is summarized in Table 2, which shows the absolute numbers of sclerites of each species, the number of specimens of each species in the samples which contained trilobites and the percentage of specimens of each species in the Raheen Formation as a whole. Old collections from the unit housed in the National Museum of Ireland (NMI), British Museum (Natural History) (BM(NH)), Geological Survey Museum (BGS GSM), Sedgwick Museum, Cambridge (SM), Birmingham University Museum (BU), Royal Scottish Museum (RSM), Trinity College, Dublin (TCD) and personal collections of Mr G. J. Murphy (now NMI) have been examined in the course of the present study but are not included in the percentage values in Table 2. Two species, both known from single specimens, *Salteria involuta* Salter and *Yumenaspis* sp., are known only from these older collections and are included in the table for the sake of completeness.

The trilobite fauna is dominated by *Tretaspis ceryx* Lamont and *Ampyx austinii* Portlock, which constitute 51·0 and 26·6% respectively of the trilobite remains in our collections. No other species exceeds 4·0% of the sample and six of the 16 each comprise less than 1%. This dominance of a trinucleid and a raphiophorid is also seen in the broadly coeval Høgberg Member of the Solvang Formation in Ringerike, Norway (Owen 1979: 250, fig. 6) and the slightly older Nakholmen Formation in Oslo-Bærum, Norway (Harper, Owen & Williams 1985). The Høgberg Member is a pure limestone and the Nakholmen Formation a black shale with dark limestone nodules and thus there is no simple relationship between litho- and biofacies. The Nakholmen Formation trilobites occur in association with an *Onniella*-dominated brachiopod fauna at the top of the formation which marks a transition from fairly deep water, possibly periodically euxinic facies, to the more ventilated conditions of the overlying Solvang Formation. Whether the trinucleid–raphiophorid association reflects a particular

Table 2 List of trilobite species, the abundance of their skeletal elements and their distribution in samples of the Raheen Formation. The single specimens of *Salteria involuta* and *Yumenaspis* sp., known only from older collections, are also listed here. The number of cephala, cranidia and lower lamellae (= free cheeks) of *Tretaspis* is given as a single feature (*). Cephala of all taxa are very rare compared with cranidia. The specimen of *Miraspis* sp. listed as complete lacks a pygidium. The total for *Homalopteon portlockii* includes four fragments of unknown position in the exoskeleton. Two indeterminate odontopleurid fragments have been omitted from the table. Sample N is from north of the Raheen Stream above the probably older strata there (see p. 92); the remaining samples are from south of the stream and their positions in the measured section are given in Table 1. Samples 2, 6, 9 and 10 did not yield any trilobite remains. (ceph.—cephala. cranid.—cranidia. fr.ch.—free cheeks. hyp.—hypostomata. thor.—thoraces. pyg.—pygidia. comp.—complete).

	Skeletal parts								Samples							
Species	ceph./ cranid.	fr.ch.	hyp.	thor.	pyg.	comp.	Total	%	1	3	4	5	7	8	N	Figs
Remopleurides sp.	–	–	1	–	–	–	1	0·1	–	1	–	–	–	–	–	15
Homalopteon portlockii (Salter)	8	–	1	9	5	–	27	3.8	2	13	1	6	4	–	1	2–8
Illaenus sp.	3	1	–	1	–	–	5	0·7	–	4	–	–	–	1	–	12
Decoroproetus sp.	2	–	–	–	1	–	3	0·4	–	3	–	–	–	–	–	13–14
Harpidella (s.l.) sp.	10	3	–	–	–	–	13	1·8	–	13	–	–	–	–	–	9
Mesotaphraspis sp. nov.	1	–	–	–	–	–	1	0·1	–	1	–	–	–	–	–	16
harpid, gen. et sp. indet.	9	–	–	–	–	–	9	1·3	–	8	–	–	–	–	1	10–11
Tretaspis ceryx Lamont	—328*—		–	9	24	5	366	51·0	–	300	3	7	19	13	24	29–40
Ampyx austinii Portlock	54	11	2	31	88	5	191	26·6	–	118	20	28	19	4	2	17–25
Salteria involuta Salter	1	–	–	–	–	–			–	–	–	–	–	–	–	27–28
Yumenaspis sp.	1	–	–	–	–	–			–	–	–	–	–	–	–	26
Sphaerocoryphe murphyi sp. nov.	2	–	1	–	3	–	6	0·8	–	6	–	–	–	–	–	42–47
Cybelinae indet., cf. '*Cybele*' *mchenryi* Reed	7	5	2	5	5	–	24	3·3	–	22	–	–	–	–	2	49–56
Flexicalymene sp. ?nov.	16	1	–	1	10	1	29	4·0	–	25	–	1	–	–	3	59–70
Calyptaulax sp.	3	–	–	1	2	–	6	0·8	–	6	–	–	–	–	–	57–58
Platylichas laxatus (M'Coy)	4	–	2	1	4	–	11	1·5	–	9	–	2	–	–	–	71–78
Primaspis aff. *caractaci* (Salter)	14	4	–	–	2	–	20	2·8	–	18	–	–	–	–	2	79–84
Miraspis sp.	4	–	–	–	–	1	5	0·7	–	4	–	–	–	–	1	85–88
						Grand total	719									

depth or substrate consistency (? soft substrates) remains debatable. Brenchley & Cocks (1982) defined two contiguous shelly associations in the upper Rawtheyan of Oslo-Asker as the *Onniella* and *Tretaspis* Associations, with the former occupying a position higher on the palaeoslope (mid-shelf) than the latter (deep shelf). Both associations are very much sparser than the Raheen fauna, and although *Tretaspis* is the dominant trilobite in the *Tretaspis* Association, and in some samples of the *Onniella* Association, raphiophorids are rare. Thus close comparisons are not possible. Excluding the trinucleid–raphiophorid dominance, the overall generic/familial composition of the Raheen fauna, including rare elements such as *Yumenaspis* and the *Salteria*, bears some similarity to associations in the lower Caradoc Balclatchie Group at Dalfask, Balclatchie and Penwhapple Burn near Girvan, south-west Scotland (Tripp 1980: table 1). These were interpreted by Tripp (1980: 135) as representing deep water environments. Similarly *Yumenaspis* in its type occurrence in the Ch'i-lien Mountains, China, is in a deep water facies (personal communication, Zhou Zhiyi, Oct. 1984). Thus a fairly deep shelf environment for the Raheen fauna seems likely.

Age

A late Caradoc to early Ashgill age was suggested for the Raheen Group by Williams (*in* Williams *et al.* 1972: 58). *Tretaspis ceryx* is very close to *T. ceriodes* Angelin (see Owen 1980), which is restricted to latest Caradoc units in Britain and Scandinavia. Similarly *Platylichas laxatus* occurs in several late Caradoc units in these areas, and the Raheen species of *Primaspis* is close to *P. caractaci* from the upper Caradoc of south Shropshire; thus the closest ties of the trilobite fauna are with the upper Caradoc. This is broadly supported by graptolites which have been examined by Dr R. B. Rickards of Cambridge University. He informs us that the presence of a climacograptid reminiscent of *Climacograptus caudatus* Lapworth and of a specimen of ?*Lasiograptus harknessi* Nicholson tentatively suggests the *Dicranograptus clingani* Zone.

Systematic palaeontology

The terminology adopted herein is largely that used by Harrington *et al. in* Moore (1959), except that of the trinucleids, which follows Hughes *et al.* (1975), and a few terms introduced since 1959 the origins of which are indicated in the text. The occipital ring is considered part of the glabella. All angles are expressed to the nearest 5° and percentage ratios to the nearest 5%.

The descriptions are based largely on our own collections but existing museum material has also been examined. Some of the older collections and literature citations involve some confusion or ambiguity as to the horizon from which specimens were collected, material from the Raheen Formation being confused with specimens from the Tramore Limestone. Where there is doubt, specimens have not been used for descriptive purposes and citations omitted from synonymy lists. The indeterminate species of *Remopleurides* (Fig. 15), *Illaenus* (Fig. 12), *Harpidella* (s.l.) (Fig. 9) and a harpid (Figs 10–11) in our collections are too poorly preserved to warrant description or discussion but are illustrated for the sake of completeness.

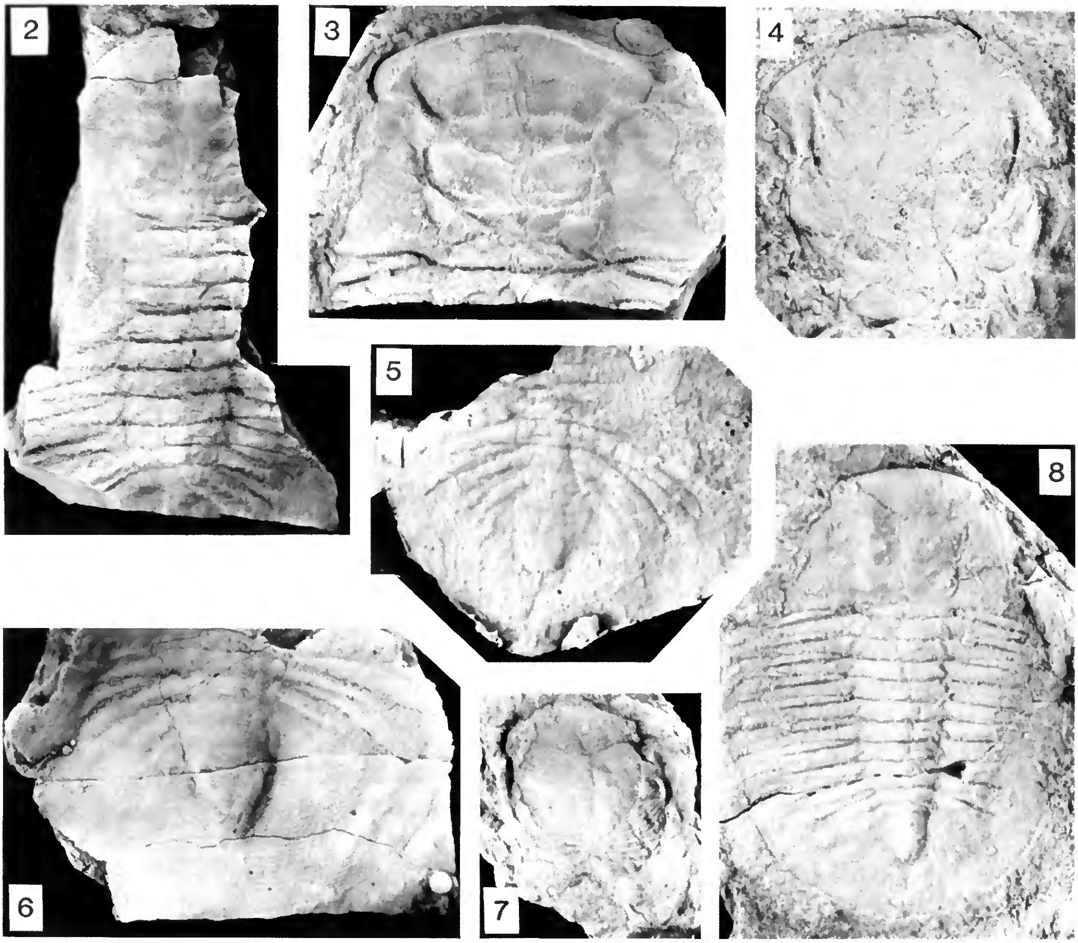
Family **NILEIDAE** Angelin, 1854

Genus ***HOMALOPTEON*** Salter, 1866

TYPE SPECIES. Subsequently designated by Vogdes, 1925; *Ogygia Portlockii* Salter, 1849: 1–4; pl. 7, figs 1–2, 6–7. From the Raheen Formation (upper Caradoc) at Newtown Head, Co. Waterford.

Homalopteon portlockii (Salter, 1849)
Figs 2–8

1843 *Asaphus dilatatus* (Dalman); Portlock: 293; pl. 24, fig. 3.
1848 *Ogygia dilatata* (Dalman); Phillips: 239.
1849 *Ogygia Portlockii* Salter (*pars*): 1–4; pl. 7, figs 1–2, 6, 7 (*non* figs 3–5, 3*–5*, = *Homalopteon radians* (M'Coy); see Whittard 1961: 227).



Figs 2–8 *Homalopteon portlockii* (Salter). Fig. 2, **lectotype** herein selected; BGS GSM266, dorsal view of internal mould of articulated specimen, × 0·9. Original of Salter (1849: pl. 7, figs 1, ?2; 1866: pl. 19, fig. 6). Fig. 3, BGS GSM35312, dorsal view of internal mould of cranidium, × $1\frac{1}{4}$. Original of Salter (1866: pl. 19, fig. 9). Fig. 4, It.17465, ventral view of hypostoma, × 3, sample 3. Fig. 5, SM A16151, dorsal view of latex cast of pygidium, × 1. Fig. 6, BGS GSM35311, dorsal view of internal mould of pygidium, × 0·9. Original of Salter (1866: pl. 19, fig. 8). Fig. 7, BGS GSM35313, ventral view of partially exfoliated hypostoma, × $1\frac{1}{2}$. Original of Salter (1866: pl. 19, fig. 10). Fig. 8, BGS GSM35310, dorsal view of internal mould of specimen lacking free cheeks, × 2. Original of Salter (1866: pl. 19, fig. 7). Raheen Formation. See p. 95.

non 1852 *Ogygia Portlockii* Salter; Barrande: 259, 271–272 (= *Homalopteon radians* (M'Coy); see Whittard 1961: 227).
1866 *Barrandia* (*Homalopteon*) *Portlockii* (Salter) Salter: 138–140; pl. 19, figs 6–10.
1899 *Barrandia Portlockii* (Salt.); Reed: 723.
1931 *Homalopteon portlockii* (Salter) Reed: 468.
1973 *Barrandia portlockii* (Salter); Hughes: fig. 3(4); p. 12.
1980 *Homalopteon portlockii* (Salter); Baird: 25.

LECTOTYPE. Here selected: BGS GSM266, an incomplete articulated specimen, original of Salter 1849: pl. 7, figs 1, ?2 and 1866: pl. 19, fig. 6. Fig. 2.

MATERIAL. Specimens of all but the free cheek of this species are present in our samples but are poorly preserved; the following description is based largely on the specimens illustrated by Salter (1849, 1866).

DESCRIPTION. Complete specimen oval in outline, maximum width half sagittal length.

Cranidium parabolic, sagittal length about two-thirds of posterior width. Glabella parallel-sided over its posterior two-thirds, in front of which it expands to 170% of its occipital width. Occipital ring lenticular in outline, sagittal length 20% of maximum width, defined anteriorly by a shallow but distinct occipital furrow. Four pairs of glabellar furrows present but as all the available cranidia show some degree of crinkling their precise development is not clear. S1 parallel proximally, turning abaxially through 90°. S4 situated just in front of the level where the glabellar expansion begins. None of furrows extend to axial furrow. Anterior part of glabella steeply declined, although this feature is commonly accentuated diagenetically. Axial furrows broad (tr.) and shallow. Fixed cheeks triangular in outline. Posterior borders moderately swollen (exsag.), transversely directed and tapering abaxially. Posterior border furrows broad and shallow, directed abaxially rearwards at a high angle to the sagittal line. Palpebral lobes crescentic, extending from a level a short distance behind S3 to a short distance in front of S4 where they abut the frontal lobe of the glabella. Free cheeks not known.

Hypostoma gently swollen (tr., sag.), very slightly longer than wide. Median body oval in outline, extending to anterior margin, defined laterally by deep furrows, and by a gentle break in slope posteriorly. Anterior wings short (tr.) but distinct. Lateral border narrow, posterior border long (sag., exsag.), flat-lying. External surface of hypostoma bearing closely-spaced terrace lines which step down forwards. With the exception of those on the anterior part of the median body, which are essentially transversely directed, the terrace lines curve in arcs which are concave forwards.

Thorax of eight segments, slightly barrel-shaped. Axis weakly swollen, occupying approximately 30% of the width of each segment, tapering very gently rearwards. Anterior and posterior edges of each axial ring very gently convex rearwards. Axial furrow no more than a slight break in slope. Pleurae transversely directed with fulcrum situated at about two-thirds of length from axis. Pleural furrow directed abaxially rearwards at a high angle to the sagittal line, dying out distally. Tips of pleurae tapered with the anterior edge curving sharply rearwards and the posterior edge deflected more gently rearwards. Closely spaced terrace lines, stepping down abaxially, developed on outer parts of pleurae, approximately parallel to the sagittal line.

Pygidium semicircular in outline in smaller specimens but sagittal length increasing to about two-thirds of maximum width in larger pygidia. Axis occupies 25% of the maximum width and 60–65% of the sagittal length of the pygidium; gently convex (tr.) anteriorly, more strongly so posteriorly. Behind the round-ended axis is a short, narrow (tr.) post-axial ridge. Four well-developed axial rings present (n = 4) and up to a further three can be discerned in addition to a short terminal piece. Three distinct pleural ribs present (n = 4) and a fourth is much less well developed. Pleural and interpleural furrows broad and shallow, dying out abaxially. Surface of outer parts of pygidium bears concentric terrace lines which step down rearwards. These are very weakly developed anteromesially.

DISCUSSION. The history of the familial assignment of *Homalopteon* was summarized by Hughes (1979: 162, 164), who discussed its distinction from *Barrandia* M'Coy, 1849. The redescription here of the type species, *H. portlockii*, confirms Hughes' conclusions. *H. portlockii* differs from *H. radians* (M'Coy, 1849) from the uppermost lower Llandeilo of Builth, central Wales, and possibly the lower Llanvirn of Shelve (see Hughes, 1979 for revision), primarily in the pygidium having more axial rings (4–7 as against 2–4) and pleural ribs (3 distinct and 1 weak as against 1 distinct and 1 weak). The glabella may be more strongly expanded frontally, the glabellar furrows may be more deeply impressed and the outline of the fixed cheek may be slightly different in the Irish species, but these may all reflect differences in preservation. As noted by Hughes (1979: 171) *H. murchisoni* Hughes, 1979 from the Llandeilo (*gracilis* Zone) of Builth is morphologically intermediate between *H. radians* and *H. portlockii.*

Family **PROETIDAE** Salter, 1864

Subfamily **TROPIDOCORYPHINAE** Přibyl, 1946

Genus ***DECOROPROETUS*** Přibyl, 1946

TYPE SPECIES. Original designation by Přibyl, 1946; *Proetus decorus* Barrande, 1846: 64. From the Liteň Formation (Wenlock), Lodenice, Prague district, Czechoslovakia.

Decoroproetus sp.
Figs 13–14

MATERIAL. Only two cranidia and one pygidium, all incomplete, are known.

DISCUSSION. Although the anterior border and fixed cheeks are poorly preserved, the distinct anterior constriction of the glabella invites comparison with *D. calvus* (Whittard) and *D. piriceps* (Ingham) from the Caradoc (Soudleyan to ?Actonian) and lower Ashgill respectively. These British species were redescribed by Owens (1973) and the age of some of the units containing *D. piriceps* recently reviewed by Price (1984). The marked abaxial taper of the occipital ring, the more tapered posterior part of the pygidial axis and the greater number of pleural furrows which are also more deeply incised distally distinguish the Raheen form from these species.

Family **DIMEROPYGIDAE** Hupé, 1953

Subfamily **MESOTAPHRASPIDINAE** Jaanusson, 1956

Genus ***MESOTAPHRASPIS*** Whittington & Evitt, 1954

TYPE SPECIES. Original designation; *Mesotaphraspis parva* Whittington & Evitt, 1954: 46–48; pl. 3, figs 1–36; pl. 4; text-fig. 11. From the Edinburg Limestone (Middle Ordovician) of Virginia, U.S.A.

Mesotaphraspis sp. nov.
Fig. 16

MATERIAL. A single external mould of a cranidium.

DESCRIPTION. Glabella occupies 70% of sagittal length of cranidium and has a maximum width directly in front of occipital furrow equal to 80% of its sagittal length. Occipital ring tapering strongly over its outer two-thirds, bearing a median tubercle. Occipital furrow transversely directed. Remainder of glabella tapering gently forwards, rounded frontally. S1 and S2 marked by shallow indentations. Axial furrow deep. Preglabellar field long (sag., exsag.), bearing a large triangular median pit in front of deep preglabellar furrow. Anterior border furrow well incised, curving in a gentle arc convex forwards. Anterior border broad (sag., exsag.). Inner parts of fixed cheeks narrow (tr.), defined abaxially by long (exsag.), deep palpebral furrows which converge forwards slightly. Posterior branch of facial suture approximately transversely directed; anterior branch curves abaxially for a short distance before being directed forwards at about 35° to the sagittal line. External surface of cranidium densely covered in coarse granules.

DISCUSSION. The narrow (tr.) inner parts of the fixed cheeks distinguish this specimen from all other described species of *Mesotaphraspis*, but until more material is available a new species is not formally established. It is closest to *M. inornata* Whittington & Evitt (1954: 48; pl. 24, figs 1–39) from the Lincolnshire Limestone (lower Caradoc?) of Virginia. However, in addition to the broader inner fixed cheek, the American species has the occipital ring only gently tapered distally.

Family **TRINUCLEIDAE** Hawle & Corda, 1847

Subfamily **TRINUCLEINAE** Hawle & Corda, 1847

Genus ***TRETASPIS*** M'Coy, 1849

TYPE SPECIES. Subsequently designated by Bassler, 1915: 1285; *Asaphus seticornis* Hisinger, 1840: 3; pl. 37, fig. 2. From the Fjäcka Shale Formation (Pusgillian) of Dalarna, Sweden.

Tretaspis ceryx Lamont, 1941
Figs 29–40

1899 *Trinucleus hibernicus* Reed (*pars*): 723.
1939 *Tretaspis* cf. *cerioides* (sic) (Angelin); Lamont *in* Stubblefield: 59
1939 *Tretaspis* cf. *cerioides* (sic) (Angelin); Lamont: 173.
1941 *Tretaspis ceryx* Lamont: 459–463; pl. 5, figs 10–14.
non 1953 *Tretaspis ceryx* Lamont; Lamont: 433 [= *Broeggerolithus* sp.].
1975 *T. ceryx* Lamont; Hughes *et al.*: 564.
1980 *Tetraspis* (sic) *ceryx* Lamont; Tunnicliff: 45.
1980 *Botrioides hibernicus* (Reed); Baird: 7 (*pars*, Newtown Head specimens only).
1980 *Tretaspis* sp.; Baird: 52 (*pars*, Newtown Head specimens only).
1981 [generically undetermined] *ceryx* Lamont; Temple: 220; table 1; fig. 9.

LECTOTYPE. Selected by Temple (1981: 220); BU 297a, an almost complete internal mould, lacking the upper lamella of the fringe.

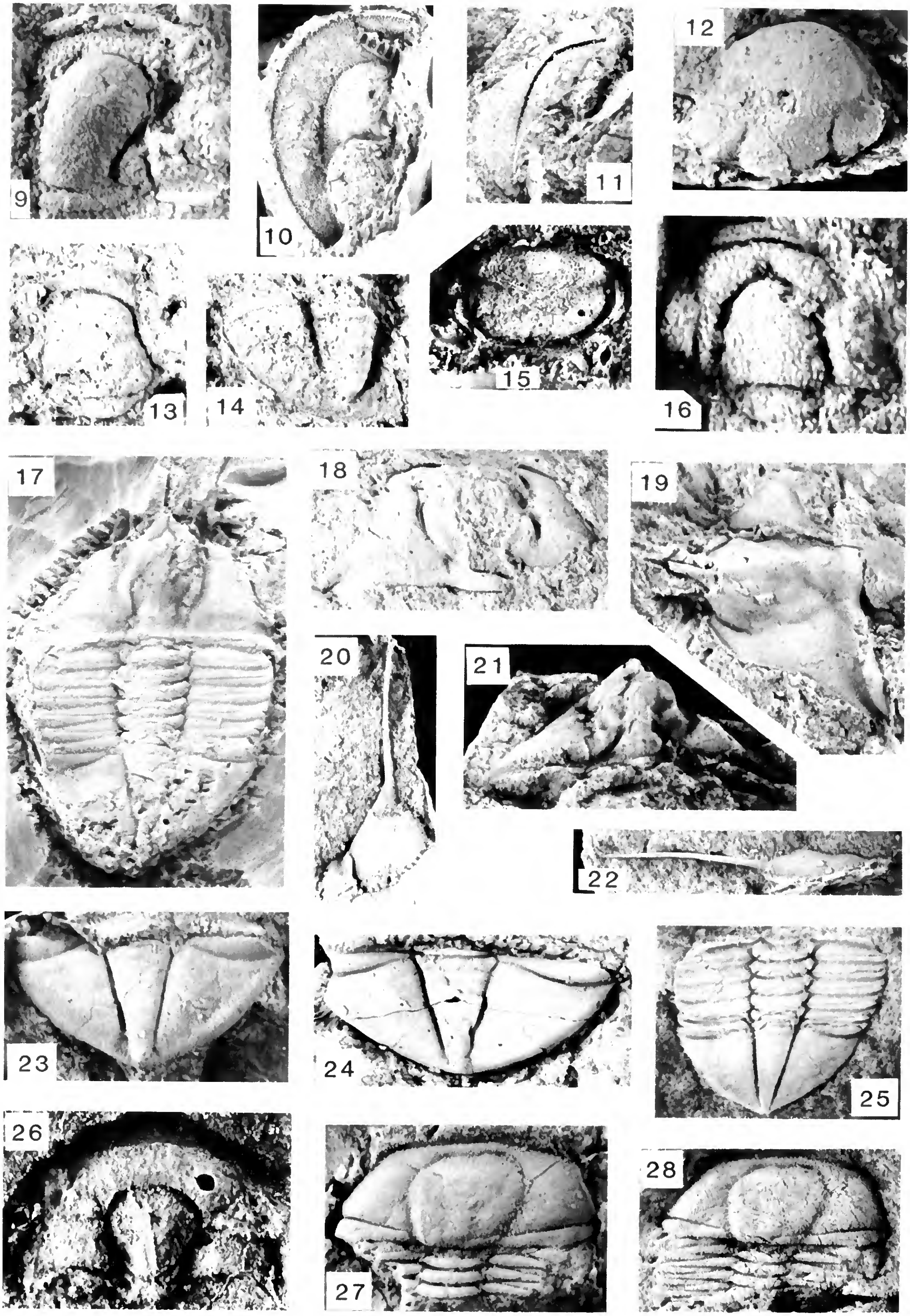
MATERIAL. Complete and disarticulated specimens of this species constitute the most abundant trilobite remains in the Raheen Formation (51% of the material sampled).

DIAGNOSIS. *Tretaspis* of the *T. moeldenensis* group with arcs E_{1-2}, I_{1-2}, I_n complete and I_3 almost invariably complete. No other arcs developed. Arcs I_1, E_{1-2} in deep, slot-like sulci over the whole fringe. External surface of glabella and genal lobes strongly reticulate. Six to seven deep pygidial apodemal pits.

DESCRIPTION. Occipital ring arched strongly rearwards and upwards. Occipital furrow shallow. Glabella between occipital ring and pseudofrontal lobe narrow and strongly convex (tr.) mesially, very weakly so laterally where the composite lateral glabellar lobe is barely discernible. S1 and S2 shallow on the external surface, deeper on internal moulds. Pseudofrontal lobe subspherical, bulbous and overhanging part of the fringe, occupying approximately 65% of the sagittal glabellar length. Median node situated slightly behind the highest part of the glabella. Axial furrows broad and shallow. Genal lobes quadrant-shaped, gently inclined from dorsal and posterior border furrows, outer parts steeply declined. Lateral eye tubercles located on the posterior parts of the genal lobes, small, more distinct on internal mould than external surface. Weak eye ridges diverge rearwards at about 120° from very shallow S3; only visible on internal mould. External surface of glabella and genal lobes bears a strong, coarse reticulation which is much more subdued on internal moulds. Furrows smooth, as is the ridge-like posterior border. Length of genal spines not known. Inner parts of fringe steeply declined, outer part more gently so.

Pit arcs E_{1-2}, I_{1-2} and I_n complete; I_3 lacks a few pits posteriorly in only one out of 109 specimens. Pits arranged in a single set of radii with those in arcs E_{1-2} and I_1 sharing deep slot-like sulci at least to the zone of complication if not to the posterior border. Weak lists developed on both sides of I_2. As Fig. 29 (p. 102) shows, there are 20–26 pits in E_1 (half fringe; $n = 41$, $\bar{x} = 23\frac{1}{2}$, S.D. $= 1\frac{1}{2}$), $17\frac{1}{2}$–$23\frac{1}{2}$ ($n = 33$, $\bar{x} = 20\frac{1}{2}$, S.D. $= 1\frac{1}{2}$) in I_n and 6–9 ($n = 84$, $\bar{x} = 8$, S.D. $= 1$) along the posterior margin of the fringe. Arc E_2 contains one less pit than E_1 in 98 out of 105 specimens; 5 specimens show the same number in both arcs and single specimens are known with two and three pits fewer in E_2. One specimen (Fig. 35) shows an indentation in the posterolateral part of the fringe affecting the outer three arcs of pits. This is similar to the damage reported by Owen (1983) in several other trinucleids.

Thorax very slightly barrel-shaped. Convex (tr.) axis occupies approximately 25% of the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width of each segment. Axial furrow very shallow. Posterior pleural band ridge-like, tapering abaxially a little. Pleural furrow broad (exsag.). Very narrow anterior band expands very slightly at the fulcrum which lies only a short distance in from the pleural tip.

Length of sub-semicircular pygidium increases from about 25% to about 30% of the maximum pygidial width over the size range present in the sample. Axis weakly convex (tr.) anteriorly, progressively less so posteriorly in which direction it tapers at about 30°. Six or seven (n = 13) pairs of deep apodemal pits present along axis; up to three very shallow pits/scars can also be distinguished in a few specimens. Anterior axial ring continuous with a strong ridge on the pleural fields and up to three very much fainter ridges may also be present. Border of pygidium broad and very steeply declined. Details of terrace line pattern not known.

DISCUSSION. The similarity of *T. ceryx* to *T. ceriodes* (Angelin) was noted by Lamont (1941: 462) and Ingham (1970: 53), with Owen (1980: 722) suggesting that the Irish form may best be regarded as a geographical subspecies of *T. ceriodes*. Angelin's species from upper Caradoc (Actonian and Onnian) units in Sweden, Norway and Britain is extremely variable in its fringe pit distribution and Owen (1980: 719–723; pl. 89; text-fig. 2) defined four 'morphs' in the Norwegian *T. ceriodes angelini* Størmer. Owen argued on the basis of the syntypes of *T. ceryx* that the Raheen form differed from his *T. ceriodes angelini* morph C only in its extensive, deep I_1, E_{1-2} sulcation. The larger sample of *T. ceryx* now available, however, enables further distinctions to be made. As Fig. 29 shows, the ranges of variation in both the E_1 and I_n arcs overlap but with *T. ceryx* having a higher mean in each case ($23\frac{1}{2}$ as against 21 in E_1; $20\frac{1}{2}$ as against $18\frac{1}{2}$ in I_n). Chi-squared tests on the radius number of the posterior pit in these arcs show that the two forms are significantly different at the 1% confidence level. Moreover, whereas only one specimen out of 109 in *T. ceryx* has I_3 incomplete posteriorly, 32 out of 39 have this condition in *T. ceriodes angelini* morph C. Thus whilst *T. ceryx* is close to *T. ceriodes*, its specific status is here retained.

Fig. 9 *Harpidella* (s.l.) sp. It.19438, dorsal view of latex cast of distorted cranidium, × 12. Raheen Formation, sample 3. See p. 95.

Figs 10–11 Harpid, gen. et sp. indet. Fig. 10, It.19439, dorsal view of latex cast of cephalon, × $3\frac{1}{2}$, sample N. Fig. 11, It.15998, dorsal view of internal mould of incomplete cephalon, × 2, sample 3. Raheen Formation. See p. 95.

Fig. 12 *Illaenus* sp. It.19440, palpebral view of internal mould of cranidium, × 5. Raheen Formation, sample 3. See p. 95.

Figs 13–14 *Decoroproetus* sp. Fig. 13, It.17458, dorsal view of internal mould of incomplete cranidium, × 7. Fig. 14, It.19441, dorsal view of internal mould of incomplete pygidium, × 6. Raheen Formation, sample 3. See p. 98.

Fig. 15 *Remopleurides* sp. It.19442, ventral view of latex cast of hypostoma, × $7\frac{1}{2}$; note that the overall morphology conforms to that of the *R. eximius* species group as defined by Tripp (1980: 125). Raheen Formation, sample 3. See p. 95.

Fig. 16 *Mesotaphraspis* sp. nov. It.17459, dorsal view of latex cast of cranidium, × 18. Raheen Formation, sample 3. See p. 98.

Figs 17–25 *Ampyx austinii* Portlock. Fig. 17, **neotype** herein designated; BM(NH) It.17432, dorsal view of specimen lacking free cheeks, × $1\frac{1}{2}$, sample 4. Fig. 18, It.19443, dorsal view of cranidium lacking most of glabella, × $2\frac{1}{2}$, sample 3. Fig. 19, It.19444, oblique anterolateral view of cranidium with damaged glabellar spine, × 3. Fig. 20, It.19445, dorsal view of latex cast of incomplete cranidium, × 2, sample 3. Fig. 21, It.19446, dorsal view of distorted cranidium, × 2, sample 3. Fig. 22, It.19447, lateral view of latex cast of incomplete free cheek, × 2, sample 4. Fig. 23, SM A16147, dorsal view of latex cast of pygidium, × 3. Fig. 24, It.19448, dorsal view of pygidium, × 2, sample 4. Fig. 25, It.17478, dorsal view of articulated thorax and pygidium, ×2, sample 3. Raheen Formation. See p. 103.

Fig. 26 *Yumenaspis* sp. Dorsal view of latex peel of plasticine cast of cranidium formerly in the Murphy collection but now lost, × $6\frac{1}{2}$. Raheen Formation. See p. 106.

Figs 27–28 *Salteria involuta* Salter. Holotype. Fig. 27, BGS GSM35713, dorsal view of cephalon and anterior part of thorax, × 4. Fig. 28, dorsal view of plasticine cast of counterpart to the holotype specimen, now lost, × $3\frac{1}{2}$. Raheen Formation. See p. 106.

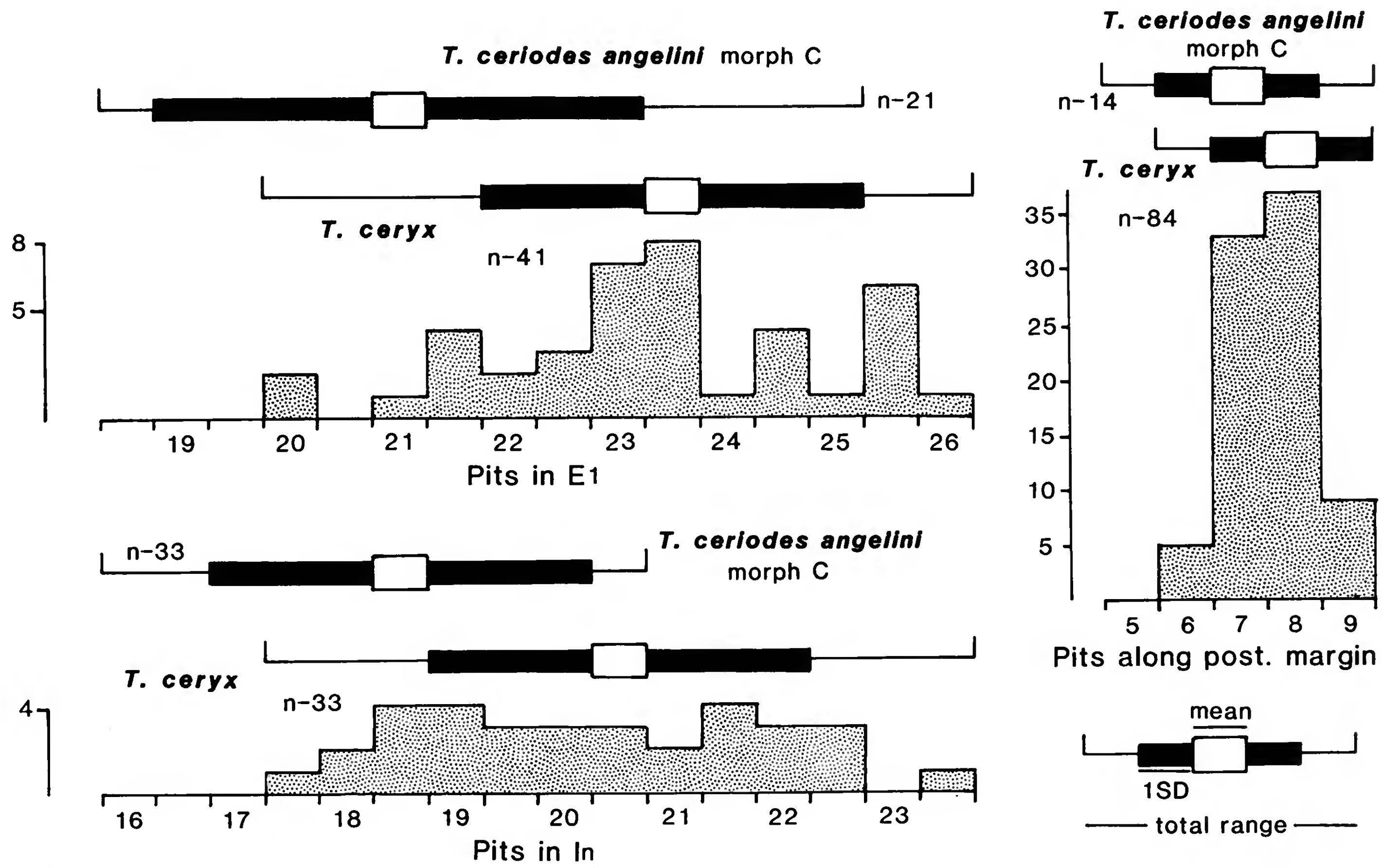


Fig. 29 Histograms showing the variation in selected fringe characters in *Tretaspis ceryx* Lamont and a comparison with the range, mean and one standard deviation each side of the mean in *T. ceriodes*-(Angelin) *angelini* Størmer morph C (see Owen 1980: fig. 2). Half-fringe values are given for the number of pits in E_1 and I_n. The number of pits along the posterior margin of the fringe excludes the posterior fossula.

The complete I_3 arc and slot-like I_1, E_{1-2} sulci of *T. ceryx* are also seen in most specimens in the topotype sample of *T. colliquia* described by Ingham (1970) from Pusgillian strata in the Murthwaite Inlier in northern England. Ingham's species was subsequently considered a subspecies of *T. moeldenensis* Cave (Price 1977: 764–770). One of Ingham's eleven original specimens has a short I_4, and two have I_3 incomplete mesially. The two specimens where the E_1 arc can be counted have 28 pits in the half-fringe whereas the maximum number in *T. ceryx* is 26, seen in one of the 41 specimens. *T. moeldenensis colliquia* also differs in having smooth genal lobes, a smooth or very subdued reticulation on the glabella and in having ten (as against six or seven) deep pygidial apodemal pits. *T. moeldenensis moeldenensis* from the lower Ashgill of Wales has an extensive I_4 arc development and a high E_1 pit count (Price 1977: fig. 1). Price (1977: 766–770) has also described samples from the lower Ashgill of Wales which he interpreted as reflecting a continuum between the topotypes of the end-member subspecies of *T. moeldenensis*. *T. caritus* Price, 1981 from the lower Rawtheyan of Wales and northern England has slot-like I_1, E_{1-2} sulci, a complete I_3 arc and seven pairs of pygidial apodemes. It differs from *T. ceryx*, however, primarily in commonly having arc I_4 developed (11 out of 15 specimens), 11–12 (as against 6–9) pits along the posterior border of the fringe, distinct lists between all the I arcs, smooth genal lobes and reticulation restricted to the posterior part of the glabella.

Lamont (1953: 433) suggested that trinucleid material in the Royal Scottish Museum, Edinburgh from Longvillian shales at Slieveroe, Co. Wicklow may be a variety of *T. ceryx*, but recent examination of this poorly preserved material shows it to belong in *Broeggerolithus*. Moreover, Brenchley *et al.* (1977: 73, 82–3; pl. 1, figs 7–9) have described specimens from there as *B.* cf. *nicholsoni* (Reed). These latter authors also recorded *T.* cf. *ceryx* from Harnagian or Soudleyan strata at Greenville, Enniscorthy, Co. Wexford. Specimens in the Griffith Collection, National Museum of Ireland, from here almost certainly belong in *Broeggerolithus*. Specimens collected by Brenchley *et al.* now housed in Trinity College, Dublin, however, are of a *Tretaspis* very close to *T. ceryx* (see Fig. 41). The material is too incomplete for confident determination but it suggests the faunal list given by Brenchley *et al.* (1977: 70) may include species from different stratigraphical levels.

Family **RAPHIOPHORIDAE** Angelin, 1854

Subfamily **RAPHIOPHORINAE** Angelin, 1854

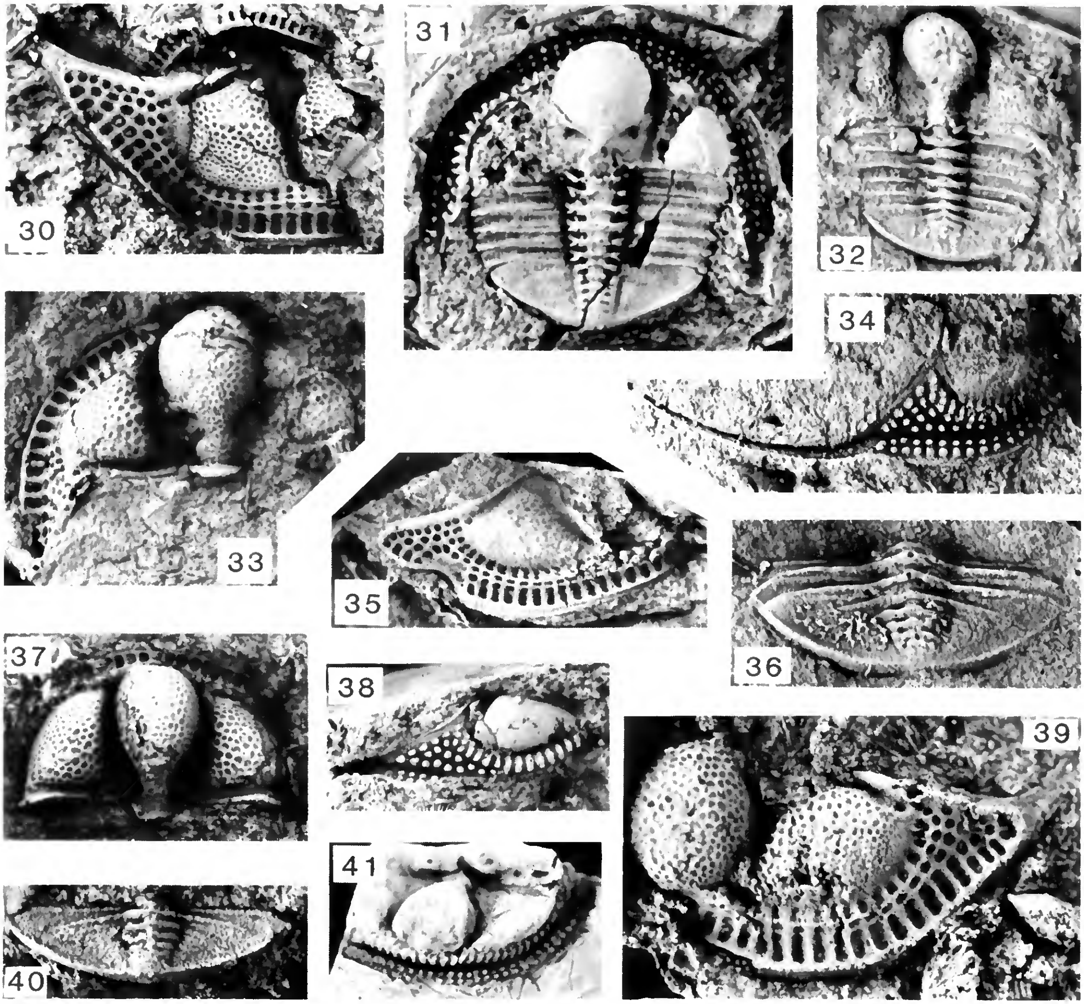
Genus ***AMPYX*** Dalman, 1827

TYPE SPECIES. By monotypy; *Asaphus* (*Ampyx*) *nasutus* Dalman, 1827: 53; pl. 5, fig. 3. From the upper Arenig of Sweden.

Ampyx austinii Portlock, 1843
Figs 17–25

1843 *Ampyx Austinii* Portlock: 261–262; pl. 1B, figs 1, 2.
1899 *Ampyx mammillatus* (sic) Sars; Reed: 723.
?1899 *Ampyx costatus* Sars; Reed: 723.
1940 *Ampyx mammillatus* (sic) Sars var. *austini* Portlock; Whittard: 157; pl. 5, fig. 4.
?1977 *Ampyx austini* Portlock; Brenchley *et al.*: 70, 82.
1980 *Ampyx linleyensis* Whittard; Baird: 3 (*pars*, Newtown Head specimens only).

NEOTYPE. A lectotype for *A. austinii* was chosen by Whittard (1940) but was destroyed during an air raid in Liverpool in 1941 (Whittard 1955: 29; personal communication Mr P. W. Phillips, Merseyside City Museums, 1981). The specimen closely conformed to the illustration on Portlock's (1843) plate 1B, fig. 2. Whittard (1940: 168) also suggested that the dorsal shield BGS GSM 35324 might be the original of Portlock's plate 1B, fig. 1 but Tunnicliff (1980: 54) noted that there is no evidence for this conclusion. There is also ambiguity as to the type horizon of *A. austinii*. Portlock (1843: 262) stated that the specimens were collected by Austin at Tramore but Whittard's lectotype was labelled 'Newtown Head' and thus was assumed by



Figs 30–40 *Tretaspis ceryx* Lamont. Fig. 30, BU 298, anterolateral view of latex cast of distorted cephalon, $\times 3\frac{1}{2}$. Cast of original of Lamont (1941: pl. 5, fig. 11). Fig. 31, lectotype, BU 297a, dorsal view of internal mould of specimen lacking upper lamella of fringe, $\times 2\frac{1}{2}$. Original of Lamont (1941: pl. 5, fig. 10). Fig. 32, It.17457, dorsal view of latex cast of articulated specimen, $\times 4\frac{1}{2}$, sample 3. Fig. 33, RSM Geol. 1870.12.864, dorsal view of latex cast of cranidium, $\times 3\frac{1}{2}$. Fig. 34, It.19449, lateral view of posterior lower lamella and spine, $\times 3\frac{1}{2}$, sample 3. Fig. 35, It.17052, anterolateral view of latex cast of cephalon showing indented fringe, $\times 3\frac{1}{2}$, sample 3. Fig. 36, It.19450, dorsal view of latex cast of pygidium and posterior two thoracic segments, $\times 4\frac{1}{2}$, sample 5. Fig. 37, RSM Geol. 1870.12.1335, dorsal view of latex cast of cranidium, $\times$ 5. Fig. 38, RSM Geol. 1870.12.1344, lateral view of internal mould of cephalon lacking upper lamella of fringe, $\times$ 2. Fig. 39, SM A16156, oblique anterolateral view of latex cast of cephalon, $\times 6\frac{1}{2}$. Fig. 40, It.19451, dorsal view of latex cast of pygidium, $\times$ 5, sample 5. Raheen Formation. See p. 99.

Fig. 41 *Tretaspis* cf. *ceryx* Lamont. TCD 20047, oblique anterolateral view of internal mould of cephalon lacking upper lamella of fringe, $\times 1\frac{1}{2}$. Caradoc strata near Greenville, Enniscorthy, Co. Waterford. See p. 103.

Whittard (1940: 20; 1955: 20) and Lamont (1941: 462–463) to have come from the Raheen Shales. The possibility that they were from the Tramore Limestone, which certainly contains an *Ampyx* close to if not conspecific with that in the Raheen Formation, cannot be excluded completely. As there is no extant type material, in order to stabilize the species a neotype (BM (NH) It.17432) from the Raheen Formation (Sample 3) is designated herein. Fig. 17.

MATERIAL. This is the second most abundant species in the Raheen fauna, comprising 26·6% of the trilobite remains sampled. Although present, free cheeks and hypostomata are rare and are less well known than the other skeletal elements.

DESCRIPTION. Cranidium (excluding spines) slightly shorter (sag.) than half its posterior width. Glabella gently convex posteriorly, a little more strongly so anteriorly; extending in front of cheeks and bearing an anterior spine of circular cross section and unknown length. A very weak carina is present in a few specimens. Long bacculae (see Fortey 1975: 15) developed, each defined adaxially by a shallow portion of the axial furrow and abaxially by a baccular furrow which is convex outwards and becomes shallower rearwards. Maximum width of glabella at (and including) bacculae approximately equal to that in front of bacculae. Occipital ring tapering gently abaxially, defined anteriorly by a broad, shallow furrow. In front of this occipital furrow the glabella tapers markedly forwards where it is separated from the posterior part of each baccula by a deep portion of the axial furrow. A generally weakly swollen glabellar lobe is developed adjacent to the anterior part of the baccula. It is confluent with the glabellar stem posteromesially but defined anteromesially by a deep furrow which is directed forwards at about 45° to the sagittal line and dies out abruptly both anteriorly and posteriorly. Axial furrow deep adjacent to frontal lobe of glabella. Fixed cheeks subtriangular in outline. Posterior border ridge-like, transversely directed over most of its length, curving rearwards and expanding slightly distally. Posterior border furrow shallow and very broad (exsag.). Facial suture sinuous, directed adaxially forwards at 50° to the sagittal line to opposite the mid parts of the bacculae, curving abaxially through 30° before turning sharply adaxially and becoming almost transversely directed. Available free cheeks and hypostomata too poorly preserved for adequate description.

Maximum width of thorax at second and third segments. First segment slightly longer (sag., exsag.) than the others and tapering markedly distally whereas the remainder are blunt-ended. Axis occupies 30% of the thoracic width anteriorly, tapering to 25% posteriorly. Axial rings moderately convex (tr.) with lobe-like swellings adjacent to the well-incised axial furrows. Pleurae flat-lying, transversely directed. Broad (exsag.) pleural furrow tapers slightly at the distal end of the first segment, but maintains its width on the other segments where it curves very gently forwards distally.

Pygidium triangular in outline with a sagittal length ranging from about 40% to about 50% of the maximum width. Axis occupies 20–25% of the anterior width and tapers rearwards at 50–60°. Lenticular articulating half-ring short (sag.). Up to five weak axial rings may be discerned in some specimens but many show no segmentation of the axis. Axial furrow deep and narrow. A single deep furrow is present on the pleural area extending in a broad arc convex rearwards, from the anterolateral corner of the axis to the lateral border a short distance behind the anterior corner of the pygidium. Border of pygidium steeply declined, not visible in dorsal view.

DISCUSSION. Whittard (1955: 18–21) suggested that *Ampyx austinii* might be synonymous with his own species, *A. linleyensis*, from strata belonging to the Llanvirn *Didymograptus bifidus* Zone at Shelve in the Welsh Borderland. He considered differences in the glabella between the Shropshire and Irish forms noted by Lamont (1941: 463) to be minor, perhaps with the exception of the narrower (tr.) glabellar stem of *A. austinii*. In addition, however, the absence of both principal genal veins and deeply incised furrows on the pygidial axis also serve to distinguish the Irish species.

Preliminary analysis of specimens from the Tramore Limestone suggests that *A. austinii* may be present and would indicate a long stratigraphical range for the species. Brenchley *et al.*

(1977) recorded *A. austinii* from the probable Caradoc strata at Greenville, Enniscorthy, Co. Wexford. The fauna here is in need of modern taxonomic study, but the presence of a trinucleid similar to the Raheen *Tretaspis ceryx* (see above) suggests that at least one horizon at Greenville may correspond to the Raheen Formation.

A. austinii differs from the type species *A. nasutus* (redescribed by Whittington, 1950) primarily in the presence of bacculae and hence the glabella does not expand evenly forwards as it does in this Arenig species. A revision of the Norwegian Ordovician raphiophorids being undertaken by Owen should clarify the relationships of *A. austinii* to the Scandinavian forms.

Subfamily **ENDYMIONIINAE** Raymond, 1920

Genus ***SALTERIA*** Wyville Thomson, 1864

Type species. By monotypy; *Salteria primaeva* Wyville Thomson, 1864: 1 of pl. 6. From the Balclatchie Group (lower Caradoc) of Girvan, south-west Scotland.

Salteria involuta Salter, 1864
Figs 27–28

1864 *Salteria involuta* Salter: 4 of pl. 6.

Holotype. The species is not present in recent collections and is known only from a single specimen in the collections of the BGS (GSM 35713) which is almost certainly the original of Salter. A plasticine cast taken some years ago from an external mould housed with the Murphy Collection in the NMI shows that this was the counterpart of the BGS specimen but the original has now unfortunately been lost.

Description. Smooth, weakly swollen glabella expanding forward to 140% of its posterior width, very gently rounded frontally. Occipital furrow absent; the 'furrow' on the right side of the specimen is a diagenetic fracture. Dorsal and preglabellar furrows weakly impressed. Fixed cheeks smooth, almost flat-lying proximally, outer parts gently declined. Posterior borders expanding gently abaxially over most of their length, tapering distally a little. Posterior border furrows diverging abaxially forward at 165°, in which direction they deepen. Preglabellar area narrow (sag., exsag.). Free cheek and hypostoma not known.

Only the anterior four thoracic segments preserved. Axial rings lenticular, tapering more markedly forwards, abutting posterior band of each pleura at an angle of about 50° to the sagittal line. Pleura transversely directed, crossed by distinct pleural furrow which is directed abaxially rearwards from the anteromesial corner at 80° to the sagittal line. The anterior band therefore expands abaxially whilst the posterior band tapers in this direction. Pygidium not known.

Discussion. A lectotype for the type species of *Salteria*, *S. primaeva* Wyville Thomson, was selected by Tripp (1980: 130), who illustrated other specimens from the lower Balclatchie Group at Girvan and included *S. americana* Cooper, 1953 from the Edinburg Formation in Virginia in its synonymy. *S. involuta* differs from *S. primaeva* in lacking distinct glabellar furrows, in having proportionally broader fixed cheeks and the posterior border not as expanded laterally.

?Family **HAPALOPLEURIDAE** Harrington & Leanza, 1957

Genus ***YUMENASPIS*** Chang & Fan, 1960

Type species. Original designation; *Yumenaspis yumenensis* Chang & Fan, 1960: 135; pl. 9, figs 1–5; text-figs 32–33 (see also Lu *et al.* 1965: 642; pl. 132, figs 1–6). From the middle Ordovician of the Ch'i-lien Mountains, China.

Yumenaspis sp.
Fig. 26

Material. A plasticine cast of a cranidium in the Murphy Collection in the NMI, original now lost.

DISCUSSION. This specimen was discussed briefly by Tripp (1976: 397), who noted that the long preglabellar field is similar to that of the type species *Y. yumenensis* but that the position of the palpebral lobe close to the glabella is similar to the condition in *Y. templei* Tripp, 1976. This last species is from the Lower Llandeilo basal Superstes Mudstones at Girvan. Tripp (1980: pl. 3, fig. 17) later illustrated an indeterminate *Yumenaspis* cranidium from the upper Balclatchie Group (lower Caradoc) at Girvan. The length of the preglabellar field and position of the palpebral lobe resemble these features in the Raheen specimen but detailed comparisons are not possible.

Family **CHEIRURIDAE** Hawle & Corda, 1847

Subfamily **DEIPHONINAE** Raymond, 1913

Genus ***SPHAEROCORYPHE*** Angelin, 1854

TYPE SPECIES. Subsequently designated by ICZN Opinion 614, 1961; *Sphaerocoryphe dentata* Angelin, 1854: 66; pl. 34, fig. 6. From the upper Ordovician of Sweden.

Sphaerocoryphe murphyi sp. nov.
Figs 42–47

?1899 *Sphaerexochus mirus* Beyr.; Reed: 723.

HOLOTYPE. A pygidium (BM(NH) It.19453) from Sample 3. Fig. 44.

MATERIAL. In addition to the holotype, two cranidia, an hypostoma and two pygidia are paratypes. The species comprises 0·8% of the Raheen trilobite fauna.

NAME. For Mr G. J. Murphy who studied the Ordovician rocks of Co. Waterford in the 1950s.

DIAGNOSIS. Species of *Sphaerocoryphe* with two profixigenal spines on the cranidium and strongly divergent posterior pygidial spines.

DESCRIPTION. Sagittal glabellar length equal to approximately half posterior cranidial width (excluding spines). Transverse occipital ring defined anteriorly by a very weakly incised occipital furrow. Basal glabellar lobes gently swollen, circular in outline, situated midway between occipital ring and spherical frontal lobe, which occupies almost two-thirds of the sagittal glabellar length. Dorsal furrows shallow on external surface, deeper on internal mould. Posterior border transversely directed. Broad-based genal spines directed abaxially rearwards at 40° to the sagittal line. Lateral border directed abaxially forwards at 40° to the sagittal line, bearing two robust profixigenal spines; the posterior of these is situated very close to the genal spine. Posterior border furrow shallow proximally, deepening abaxially and confluent with the lateral border furrow. Field of fixed cheek gently swollen (tr., exsag.). Palpebral lobe forwardly placed. External surface of frontal glabellar lobe bears a dense subdued granulation. Rest of external surface too poorly preserved for sculpture to be discerned. Free cheek not known.

Hypostoma trapezoidal in outline. Median body swollen (tr., sag.), slightly longer than wide, defined by broad furrows which are deep laterally but shallow anteriorly and posteriorly. Middle furrow and posterior lobe effaced. Posterior border broad (sag., exsag.) and flat-lying; lateral borders taper forwards and are steeply inclined. Anterior wings transversely directed.

Thorax unknown. Pygidium, excluding spines, sub-semicircular in outline. Axis poorly differentiated from pleural regions, bearing four rings and a triangular terminal piece. Non-functional half-rings present behind the first and second axial rings. The anterior two rings are confluent with pleural ribs which broaden abaxially, bear weakly incised furrows proximally and are extended as broad spines. The anterior pair of spines are gently divergent proximally, curving rearwards through about 30° over their outer 40% where they taper markedly. Posterior spines long, very robust, diverging rearwards at 70° proximally, becoming a little more parallel distally. The posterior spines taper evenly and extend to a level behind the posterior border equal to at least twice the sagittal pygidial length. There is a slight break in slope between the first two axial rings and the pleural ribs. No such differentiation is visible on the

posterior two rings/ribs which, together with the terminal piece, extend to the broad (sag., exsag.) posterior border which curves in a gentle arc convex rearwards. External surface of pygidium densely covered in fine granules.

DISCUSSION. The most important discriminatory feature is the presence of two profixigenal spines. Other described species sharing this character are: *S. pemphis* Lane, 1971 from the Balclatchie Group (low Caradoc), Girvan district; *S. ludvigseni* Chatterton, 1980 from the Esbataottine Formation (Llandeilo) of the Mackenzie Mountains; *S. thomsoni* (Reed, 1906) from the Upper Drummuck Group (high Rawtheyan), Girvan district; *S.* cf. *thomsoni* (Reed) of Lane, 1971 from the Ashgill Series, Norber Brow, northern England; *S. kingi* Ingham, 1974 from the Rawtheyan Zones 6 and 7 of northern England; and *S.* aff. *kingi* Ingham of Owen, 1981 from horizons of Cautleyan to Rawtheyan age in the Oslo region, Norway. *S. murphyi* differs from these species in its more strongly divergent posterior pygidial spines, and the rounded posterolateral angles of the hypostoma. The closest resemblance is to *S. pemphis*, which it resembles in its large size, robust downturned profixigenal spines, short hypostoma with effaced posterior lobes and long anterior pygidial spines.

Family **ENCRINURIDAE** Angelin, 1854

Subfamily **CYBELINAE** Holliday, 1942

DISCUSSION. The large discrete glabellar lobes and the pygidial ring and rib development suggest an affinity between the Raheen cybeline and species currently placed in *Deacybele* Whittington, 1965. Owen & Romano (*in* Harper *et al.* 1984) have noted that the generic status of Whittington's taxon is questionable, and a preliminary multivariate analysis of the Cybelinae by R. P. Tripp, J. T. Temple & A. W. Owen confirms this. Until this analysis is complete, the Raheen form is not ascribed to an existing genus.

Cybelinae indet., cf. ***'Cybele' mchenryi*** Reed, 1899[1]
Figs 49–56

?1846 *Encrinurus stokesii* M'Coy: 47 (*pars*, Newtown Head material only).
cf. 1899 *Cybele McHenryi* Reed: 751; pl. 49, fig. 7.
?1899 *Cybele rugosa* Portl.; Reed: 752.

MATERIAL. Disarticulated examples of all the exoskeletal elements of this species together comprise 3·3% of the trilobite fauna.

DESCRIPTION. Sagittal length of cranidium equal to about 30% of maximum width. Glabella convex (tr.), width across L1 85–90% maximum width across frontal lobe. Occipital ring arched gently forwards mesially, tapering a little distally where it is deflected gently rearwards behind L1 before terminating slightly beyond the level of L1. Mesial part of occipital ring not sufficiently well preserved to determine whether a median tubercle is present or not. Occipital furrow shallow mesially, deepening into an elongate apodeme behind L1. L1 almost square in outline and, with L2, strongly depressed compared with the transversely convex central lobe. S1 deep and pit-like proximally, shallowing and transversely directed towards axial furrow. L2 transversely rectangular in outline, longer (tr.) than L1 but approximately as wide (exsag.). S2 transverse, narrow and deep, expanding (exsag.) proximally and deepening into apodeme. L3 largest of lobes, being about twice as wide (exsag.) as either L1 or L2. Outer edge of L3 directed gently adaxially forwards to sagittal line. S3 directed abaxially forwards at 60°, narrow proximally, broadening slightly before joining axial furrow. Frontal lobe occupies at least 40% of sagittal glabellar length, broadly rounded anteriorly, median pit absent. Preglabellar area not known. Axial furrow broad and shallow; fossula midway between S3 and anterior branch of facial suture. Posterior border ridge-like, transversely directed and expanding only slightly abaxially. Genal spine parallel to sagittal line, length unknown. Posterior border furrow deep

[1] But see Recommendation 21 (a) (I.C.Z.N. 1985: 197). It is not made clear whether this ought to be applied retrospectively.

over most of its length, becoming shallower at genal angle. Field of fixed cheek rising steeply from dorsal and posterior border furrows, extended as a nearly vertical palpebral stalk opposite S2; width across L2 45% width between palpebral lobes. Distinct eye ridge directed from axial furrow at anterior end of L3 to base of palpebral stalk. Details of facial suture not known. Surface of cranidium (including internal mould), excluding furrows, densely granular, granules smallest and densest on palpebral stalk. Three pairs of slightly larger granules distinguishable opposite S2 and two pairs on frontal lobe.

Free cheek convex and steeply downturned. Field broad and gently convex. Lateral border uniformly narrow, 25% maximum width of field. Lateral border furrow broad and shallow, widening but incomplete anteriorly. Details of eye stalk and eye not known. Surface densely and evenly granular, as cranidium.

Hypostoma known from two poorly preserved, incomplete specimens which show a broad similarity to that ascribed to *Deacybele* by Owen & Romano (*in* Harper *et al.* 1984: fig. 58).

Pygidium known in detail only from internal moulds; about as long as maximum width. Axis narrowing abruptly posterior to first ring, then tapering very gently rearwards, extending for 80% length of pygidium; composed of over 20 rings, of which only the anterior is complete on internal mould. Most if not all rings bear small tubercles, sparsely scattered granules on smooth mesial strip of axis. Post-axial ridge comparatively long. Axial furrow moderately deep and narrow for most of length, shallower opposite first ring and posteriorly. Distinct break in slope between convex (tr.) axis and almost flat-lying inner part of pleural area. Pleural lobe composed of four pairs of pleurae. First composed of subequal posterior and anterior bands separated by a strong pleural furrow. Second composed of a strong posterior band and a narrower (exsag.) depressed anterior band, which dies out well before margin; pleural and interpleural furrows subequal. Third and fourth posterior bands successively narrower; third anterior band indistinct, fourth absent. First posterior band confluent with first axial ring, proximally directed at 60° to the sagittal line, curving abaxially in a broad arc through about 180° before turning very slightly adaxially, ending opposite apex of axis. Posterior rib parallel to axial furrow, intervening ribs gradational between first and fourth. Posterior bands apparently extend as short spines, ending *en échelon*. Ends of third and fourth pleurae partially fused. Posterior bands of pleurae tuberculate; pleural lobe otherwise smooth.

DISCUSSION. The Raheen cranidia most closely resemble that of '*Cybele*' *mchenryi* Reed, 1899, the holotype of which has recently come to light and is figured here (Fig. 48). Reed (1899: 752) gave the locality for this specimen (whose collector is not known) as Newtown Head, thus suggesting the Raheen Formation as the type horizon. However, the specimen is preserved in a dark limestone, a lithology not encountered in the section south of the Raheen Stream. It seems likely, therefore, that it is from the Tramore Limestone. The Raheen material differs primarily in the posterior border remaining narrow and ridge-like over most of its length; that of Reed's specimen expands from a short distance away from the occipital ring. The extent to which this simply reflects variation in one species will be assessed when the trilobites of the Tramore Limestone are described.

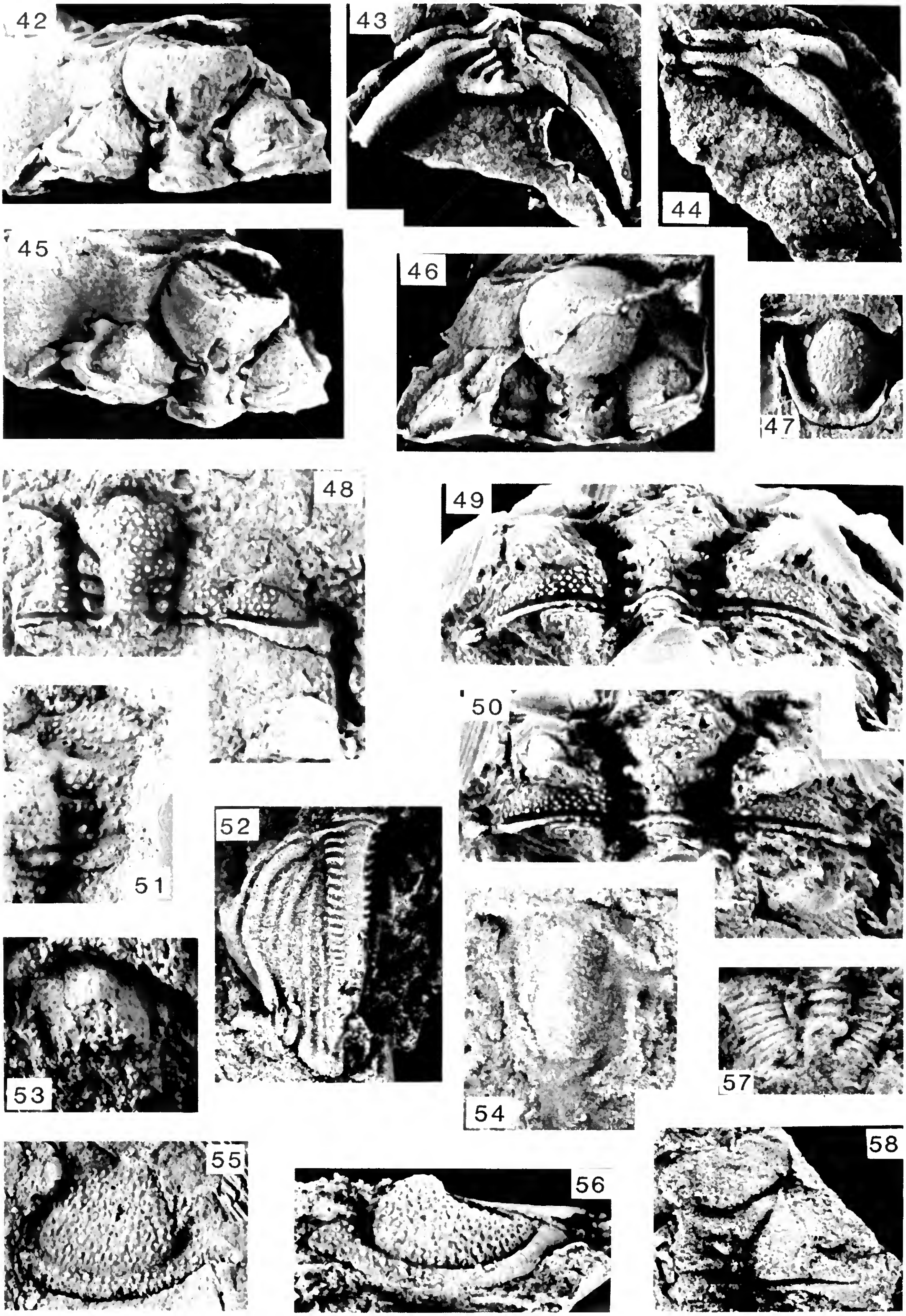
There is also a strong similarity to '*Deacybele*' *gracilis* (Nikolaisen, 1961) (see also Owen & Bruton 1980: 29; pl. 8, figs 14–17) from the highest Caradoc and basal Ashgill of the Oslo Region, Norway. The Raheen form differs in having longer S3 furrows, the posterior cranidial border only expanded distally and in having a shorter post-axial area on the pygidium. The anterior part of the cranidium is not known in the Raheen material but '*C.*' *mchenryi* has a median projection with three spines on it; '*D.*' *gracilis* has a single, robust tubercle.

Family **CALYMENIDAE** Milne Edwards, 1840

Subfamily **FLEXICALYMENINAE** Siveter, 1977

Genus ***FLEXICALYMENE*** Shirley, 1936

TYPE SPECIES. Original designation; *Calymene Blumenbachii* var. *Caractaci* Salter, 1865: 96; pl. 9, fig. 3. From the middle Caradoc of South Shropshire, England.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DISCUSSION. The status of *Reacalymene* Shirley, 1936 (type species *Reacalymene limba* Shirley, 1936) has been the subject of some debate (see Siveter 1977: 375), with most modern workers regarding it as a subgenus of *Flexicalymene*. Whittington (1965: 58) advocated that the name be restricted to the type species, and while Siveter (1977: 375) placed other species in the subgenus, he noted that it was 'most unlikely' that *F.* (*Reacalymene*) represented 'an evolutionary lineage separate from the nominate subgenus'. Siveter argued that there was a more distinct break in slope defining the posterior edge of the anterior border of the cranidium in species of *F.* (*Reacalymene*) than in other *Flexicalymene* species. The great intraspecific variability of the preglabellar area has been noted by several authors (e.g. Whittington 1965, Temple 1975, Siveter 1977) and Ingham (1977: 91) recorded an extreme variant of *Flexicalymene onniensis* Shirley *lata* Ingham with a frontal morphology like that of '*Reacalymene*'. In view of this, although the Raheen material described below has a frontal morphology approaching that of *F. limba*, the term '*Reacalymene*' is not used even at subgeneric level.

Flexicalymene sp. ?nov.
Figs 59–70

?1899 *Calymene duplicata* Murch.; Reed: 723.

MATERIAL. This is the third most abundant species in the Raheen Formation, comprising 29 specimens (4·0% of the sample), which include all parts except the hypostoma.

DESCRIPTION. Cranidium slightly more than twice as wide as long. Blunt-ended glabella subparabolic in outline, occupying 80–85% of sagittal length of cranidium. Glabella tapers gently and evenly forwards, such that its width at L3 is about 80–85% of that at L1. Occipital ring occupies 15% of sagittal glabellar length, tapering to about half its mesial width behind L1. Occipital furrow transversely directed mesially, where it is shallow on the external surface but deep on internal moulds; it deepens behind L1 where it curves gently abaxially rearwards then slightly forwards to the axial furrow. L1 longer (exsag.) than wide (tr.); suboval to angular in outline, occupying about 55–60% of the glabellar width and defined adaxially by a shallow longitudinal furrow from S1 to the occipital furrow. S1 directed adaxially rearwards at about 65–70° to the sagittal line from the dorsal furrow, turning rearwards through about 120° behind the anteromesial part of L1; a short extension of this proximal portion of S1 extends behind the posteromesial part of L2. A shallow longitudinal furrow connects this part of S1 with S2, and thus L2 is completely circumscribed by furrows and is approximately circular in outline. S2 transversely directed distally, bifurcating adaxially to define the anteromesial part of L2 and posteromesial part of L3. S3 short (tr.), transversely directed, barely discernable on

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Figs 42–47 *Sphaerocoryphe murphyi* sp. nov. Figs 42, 45, 46, It.17461a, b, dorsal and oblique dorsal views of internal mould of cranidium, dorsal view of latex cast of external mould, all × 2. Fig. 43, It.19452, dorsal view of latex cast of distorted pygidium, × 2½. Fig. 44, **holotype,** BM(NH) It.19453, dorsal view of latex cast of incomplete pygidium, × 2. Fig. 42, It.17460a, ventral view of internal mould of hypostoma, × 3. Raheen Formation, sample 3. See p. 107.

Fig. 48 '*Cybele*' *mchenryi* Reed. Holotype, GSI:F01311, dorsal view of internal mould of cranidium, × 4. Original of Reed (1899: fig. 7). Probably Tramore Limestone Formation, Co. Waterford. See p. 109.

Figs 49–56 Cybelinae indet., cf. '*Cybele*' *mchenryi* Reed. Figs 49, 50, It.19454, oblique dorsal and true dorsal views of internal mould of cranidium, both × 4, sample 3. Fig. 51, It.19455, dorsal view of latex cast of incomplete cranidium, × 6, sample N. Fig. 52, It.17480, dorsal view of internal mould of pygidium, × 6, sample 3. Fig. 53, It.19456, ventral view of internal mould of incomplete hypostoma, × 7, sample 3. Fig. 54, It.17477, ventral view of internal mould of distorted hypostoma, × 6, sample 3. Fig. 55, It.17456, lateral view of internal mould of incomplete free cheek, × 6, sample 3. Fig. 56, It.19457, lateral view of free cheek lacking eye, × 4, sample 3. Raheen Formation. See p. 108.

Figs 57–58 *Calyptaulax* sp. Fig. 57, It.17472, dorsal view of incomplete cranidium, × 6. Fig. 58, It.17471, dorsal view of incomplete internal mould of cranidium, × 4½. Raheen Formation, sample 3. See p. 114.

external surface, more deeply impressed on internal moulds where the small, circular L3 is more clearly developed. Some internal moulds show a very weakly developed L4. Glabella narrows only very slightly in front of L3. Axial furrows deep, converging forward at 20–25°. Preglabellar area comprising a preglabellar furrow and a ridge-like anterior border; there is commonly, but not invariably, a distinct change in slope between the two. Anterior border maintains its width except at its distal extremities, where it tapers. In profile the border varies from curved to more flat-topped. Posterior border expands (exsag.) abaxially, defined anteriorly by a border furrow which is narrow and deep proximally, becoming broader and much shallower abaxially. Mid-length points of palpebral lobes situated opposite L2 but the distortion of many specimens makes this difficult to assess. Anteriorly the fixed cheek field extends to opposite or slightly in front of the end of the glabella. Posterior branch of facial suture directed transversely or even forwards slightly over most of the genal field; curving gently rearwards laterally it cuts the lateral border a short distance in front of the genal angle. Anterior branch virtually parallel to sagittal line over most of its length, curving adaxially forwards across the anterior border. Free cheek almost quadrant-shaped. Border and broad shallow border furrow maintain their width over the entire outer arc of the cheek. Eye socle defined abaxially by a broad, very shallow depression. External, and to a lesser extent internal, surface of cephalon densely covered by fine granules. Hypostoma not known.

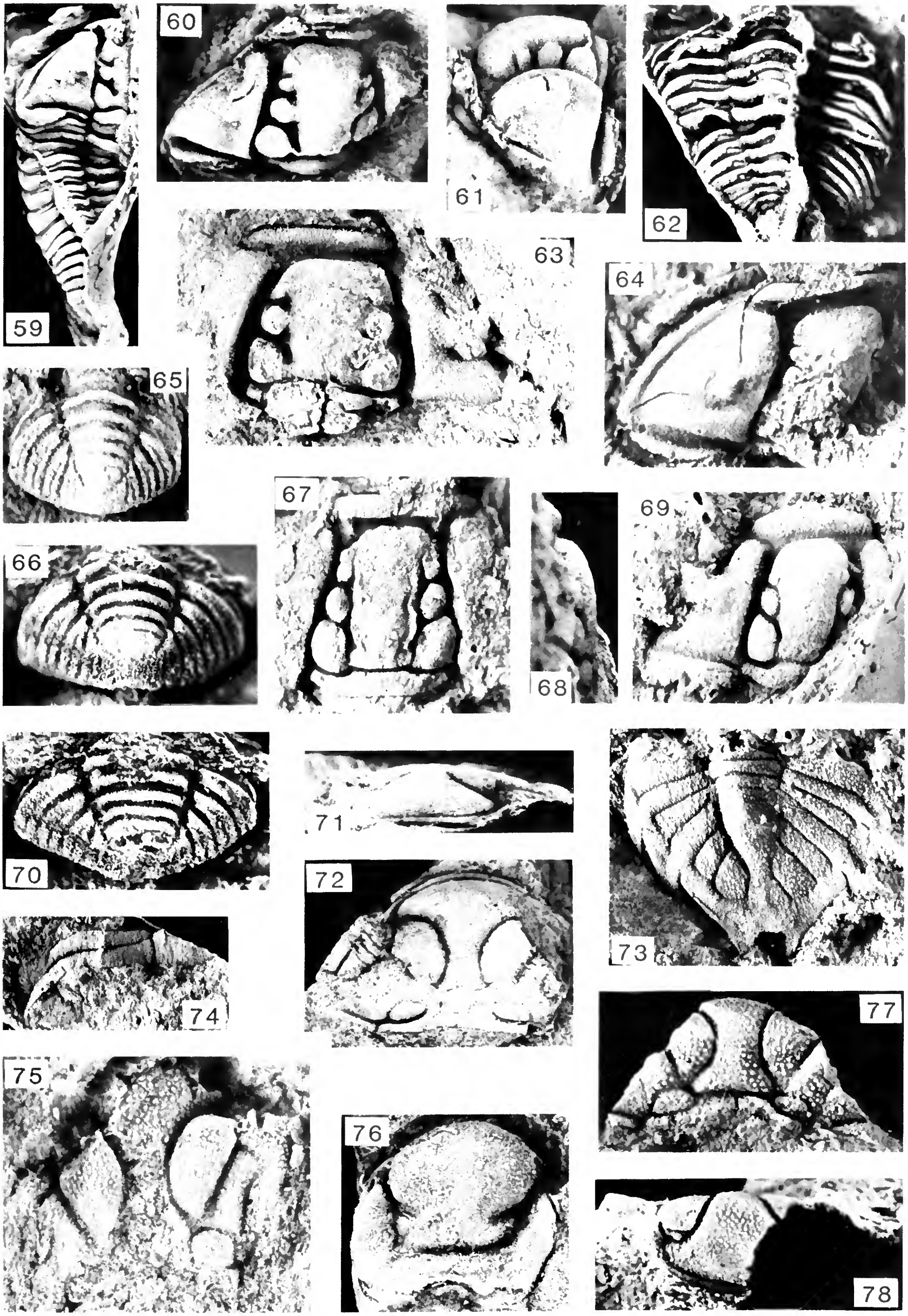
Thorax of 13 segments. Axis strongly convex (tr.); articulating half-rings equal in length (sag.) to about 50% of that of the rings. Axial furrows narrow (tr.) and shallow, but mark a distinct change in slope. Pleurae with deep furrows defining a broad (exsag.) posterior band and a narrower anterior band. The latter expands at the fulcrum to form an articulating boss. Abaxially from the fulcrum each segment is deflected steeply downwards and gently rearwards, curving gently forwards distally. External surface of thorax, excluding furrows, bears a fine, dense granulation.

Pygidium strongly convex (tr., sag.). Maximum width of axis half that of pygidium. Axis moderately convex, tapering rearwards at about 30–40°; it is blunt-ended and comprises six rings and a short terminal piece. Ring furrows deep, arched very gently forwards. Axial furrows deep except posteriorly. Anteromesial parts of pleural lobes gently declined; anterolateral and posterior parts steeply so. Four ribs and a broad (tr.) post-axial area present. Pleural furrows broad and distinct; interpleural furrows narrow, becoming shallower and in some instances dying out adaxially. External surface, and internal mould, of pygidium excluding furrows densely covered by fine granules.

Discussion. The well-differentiated anterior border in most of the Raheen cranidia suggests an affinity with species previously placed in '*Reacalymene*', the type species of which, *R. limba* Shirley from the Soudleyan of north Wales, was redescribed by Whittington (1965: 58–59; pl. 16,

Figs 59–70 *Flexicalymene* sp. ?nov. Fig. 59, It.19458, dorsal view of latex cast of incomplete articulated individual, × 2, sample 3. Figs 60, 61, It.17488, dorsal and lateral views of incomplete distorted cranidium, both × 3, sample 3. Fig. 62, It.19712, dorsal view of latex cast of incomplete thorax and pygidium, × 3½, sample 5. Fig. 63, It.17732, dorsal view of internal mould of incomplete cranidium, × 4, sample 3. Fig. 64, It.19459, dorsal view of internal mould of incomplete cephalon, × 3½, sample 3. Fig. 65, It.19460, dorsal view of internal mould of narrow pygidium, × 7½, sample 3. Figs 66, 70, It.19461, dorsal view, × 6, and view normal to axial terminal piece, × 6½, of broad pygidium, sample 3. Fig. 67, It.17464, dorsal view of internal mould of incomplete flattened cranidium, × 3½, sample 3. Figs 68, 69, It.19462, lateral and dorsal views of latex cast of incomplete cranidium, both × 5½, sample 3. Raheen Formation. See p. 111.

Figs 71–78 *Platylichas laxatus* (M'Coy). Figs 71, 72, It.17468, frontal and dorsal views of internal mould of incomplete cranidium, both × 2. Fig. 73, It.19463, dorsal view of latex cast of pygidium, × 4. Fig. 74, It.17453, dorsal view of latex cast of incomplete thoracic segment, × 3½. Fig. 75, It.17473, dorsal view of internal mould of incomplete cranidium, × 6. Fig. 76, It.17482, ventral view of internal mould of hypostoma, × 4½. Figs 77, 78, It.19464, dorsal and frontal views of internal mould of distorted incomplete cranidium, both × 6. Raheen Formation, sample 3. See p. 115.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figs 9–20). As in the Raheen sample, the Welsh species shows a range of cranidial morphology, but the Irish form differs consistently in having a more blunt-ended glabella which tapers less strongly. *F. limba* also commonly has a more evenly tapered anterior border, although one specimen illustrated by Whittington (1965: pl. 16, fig. 10) approaches the condition seen in the Irish cranidia. The shape of L1 in some of the Irish cranidia approaches the angularity considered by Whittington to be characteristic of *F. limba*, but others are much more oval in outline. None of the Welsh cranidia have L4 present. Whittington regarded the absence of interpleural furrows on *F. limba* pygidia as a feature distinguishing it from *F. pusulosa* (see below), but they are clearly visible on one of the specimens he illustrated (pl. 16, figs 19, 20).

Like the Raheen form, a blunt-ended glabella and a weakly developed L4 are also seen in *F. pusulosa* (Shirley), from the Costonian of south Shropshire, which was placed in *Reacalymene* by Shirley (1936). The holotype was reillustrated by Dean (1963: pl. 37, figs 9, 11). *F.* sp. ?nov. differs from the Shropshire species in having the glabella markedly broader at L4 than at L3, and the anterior border is less tapered and not as flat. A pygidium illustrated by Dean (1963: pl. 37, fig. 12) also has seven axial rings, as against six in the Irish specimens. Siveter (1977: 375–377, figs 10A–D) described a cranidium from the Oslo region as being close to *F. pusulosa*. Most of the features cited by Siveter as distinguishing it from *F. pusulosa* also differentiate it from the Raheen material. As Siveter suggested, the horizon of the Norwegian specimen is somewhat problematical. The cranidium is from Ballangrud in Hadeland, but the stated horizon, the late Caradoc 'Upper Chasmops Limestone' (= Solvang Formation) does not crop out there. Other museum specimens similarly labelled are of species clearly from the Ashgill Kjørrven Formation or Grina Shale Member of the Lunner Formation (see Owen 1978 for stratigraphy) which accord with recent mapping in the area.

Indeterminate material of *Flexicalymene* described by Siveter (1977: 355–356, figs 10I, K) from the 'Lower Chasmops Shale' (low Caradoc) of the Oslo region includes a cranidium with a glabellar shape and preglabellar area similar to that of *F.* sp. ?nov. It differs, however, in having a coarser external granulation; L1 and L2 are less well circumscribed by furrows and S3 more deeply impressed.

F. planimarginata Reed, 1906 (see also Whittington 1965: 60–61; pl. 17, figs 8–13, 16, 17, 20–22) from Longvillian strata in Wales and the Welsh Borderland has a blunt-ended glabella like that of *F.* sp. ?nov., but the glabella of the latter is less tapered and the preglabellar area shorter (sag., exsag.).

Family **PTERYGOMETOPIDAE** Reed, 1905

Subfamily **PTERYGOMETOPINAE** Reed, 1905

Genus *CALYPTAULAX* Cooper, 1930

TYPE SPECIES. Original designation; *Calyptaulax glabella* Cooper, 1930: 388–389; pl. 5, figs 9–11. From the Matapédia Group (Ashgill), Percé, Quebec, Canada.

Calyptaulax sp.
Figs 57–58

MATERIAL. Three cranidia, a thoracic segment and two pygidia, all poorly preserved, comprising 0·8% of the Raheen trilobite fauna.

DISCUSSION. Whilst the cranidia placed here undoubtedly belong in *Calyptaulax*, the more complete of the two pygidia is unusual in showing the rib furrows (= interpleural furrows) extending to the axial furrows—a feature more characteristic of other pterygometopids such as *Achatella* Delo, 1935 (see Ludvigsen & Chatterton 1982) and members of the Chasmopinae (see McNamara 1980, 1980a).

The strongly geniculate S3 may partially reflect compactional deformation, but it resembles the condition in *C.* aff. *norvegicus* Størmer of Whittington (1962: pl. 2, figs 17, 18) and *C. planiformis* Dean, 1962 (see also Owen & Bruton 1980: 34) from the Ashgill of Wales and northern England. Both may prove to belong in *C. norvegicus* (see Owen 1981: 63–64) which in turn is close to the type species, *C. glabella* (see Ludvigsen & Chatterton 1982: 2192–2194).

Family **LICHIDAE** Hawle & Corda, 1847

Subfamily **HOMOLICHINAE** Phleger, 1936

Genus ***PLATYLICHAS*** Gürich, 1901

TYPE SPECIES. Original designation; *Lichas margaritifer* Nieszkowski, 1857: 568; pl. 1, fig. 15. From the Porkuni Limestone (upper Ashgill) of Estonia.

Platylichas laxatus (M'Coy, 1846)
Figs 71–78

1846 *Lichas laxatus* M'Coy: 51; pl. 4, fig. 9.
1854 *Lichas sexspinus* Angelin: 74; pl. 38, figs 7–8a.
1854 *Lichas aculeatus* Angelin: 75; pl. 38, figs 7, 7a.
1899 *Lichas laxatus* M'Coy; Reed: 723.
1958 *Platylichas laxatus* (M'Coy) Tripp: 579; pl. 85, figs 3, 4 (*non* fig. 5, = *P. nodulosus* M'Coy)
1963 *Platylichas laxatus* (M'Coy); Dean: 235–237; pl. 43, figs 1, 2, 5, 8–12.
1979 *Platylichas laxatus* (M'Coy); Hurst: 204, fig. 16.5.
1979a *Platylichas laxatus* (M'Coy); Hurst: 210, fig. 41.
1980 *Platylichas laxatus* (M'Coy); Owen & Bruton: 34–35; pl. 10.

For more complete synonymy lists of this species see Dean (1963) and Owen & Bruton (1980).

MATERIAL. Cranidia, hypostomata, a thoracic segment and pygidia of this species constitute 1·3% of the Raheen fauna.

DISCUSSION. Cranidia from the Raheen Formation agree closely with those of *P. laxatus* from the type locality, Ballygarvan Bridge (see Tripp 1958: pl. 85, figs 3, 4). The length/width ratio shows considerable variation at both localities and there are no consistent differences. Other parts have not been described from Ballygarvan Bridge but are present in the Tripp collection at the BM(NH). Those from Raheen and specimens associated with *P. laxatus* cranidia elsewhere (see e.g. Dean 1963, Owen & Bruton 1980) are identical to the Ballygarvan Bridge material.

P. laxatus is an extremely common and variable species in upper Caradoc units in the British Isles and Scandinavia. The variability affects particularly the degree of inflation of the bullar lobes (see Temple 1972) in relation to the central lobe and the width and outline of the anterior border. This cranidial variability may even encompass or at least overlap with the morphologies of *P. nodulosus* (M'Coy, 1851), *P. glenos* Whittington, 1962 and *P. noctua* Price, 1980, but further study is required to establish whether these forms should be reassigned to *P. laxatus*. *P. thraivensis* (Reed, 1935: see Tripp 1958: 579) from the Rawtheyan Starfish Beds of Girvan is allied to *P. laxatus* but differs in its more posteriorly placed palpebral lobes.

Family **ODONTOPLEURIDAE** Burmeister, 1843

Subfamily **ODONTOPLEURINAE** Burmeister, 1843

Genus ***PRIMASPIS*** Richter & Richter, 1917

TYPE SPECIES. Original designation; *Odontopleura primordialis* Barrande, 1846: 29. From the Letná Formation (Caradoc) in Bohemia. (See Chatterton & Perry 1983: 33 and Ramsköld 1984: 241 for discussions of the genus.)

Primaspis aff. ***caractaci*** (Salter, 1853)
Figs 79–84

MATERIAL. Cranidia, free cheeks and pygidia constitute 2·8% of the Raheen trilobite fauna.

DISCUSSION. *Primaspis caractaci* (Salter) from the Marshbrookian and Actonian of south Shropshire was redescribed by Dean (1963: 239–241; pl. 44, figs 3, 7, 9, 11, 13, 14). The overall cranidial proportions of the Raheen material are very similar to those of Salter's species except that the glabella is proportionally broader and less tapered in front of L2. The pygidium may

differ slightly in having three rather than two spines outside the large major spines, but the third (anteriormost) spine is very small in the Raheen form, and thus may simply not be preserved in the Shropshire specimens. As Dean noted (1963: 240–241) the cranidium of *P. caractaci* is broadly comparable with that of the Harnagian *P. harnagensis* (Bancroft, 1949) also from Shropshire, but the latter species may be distinguished primarily by the presence of four outer and two inner pairs of pygidial spines in addition to the primary spines. *P. caractaci* and the Raheen form both have three pairs of inner spines, the outer of which is not fused with the primary spines. This contrasts with the condition in *P. evoluta evoluta* (Törnquist) from the Ashgill of Sweden, north Wales and possibly Norway (see Owen 1981: 69) where the anteriormost of the three is fused with the base of the primary spines.

P. semievoluta (Reed, 1910) from the Longvillian of the north of England (see Dean 1962: 122; pl. 17, figs 3, 10, 11, 13, 15) has a very strongly tapering occipital ring and only two pairs of spines between the primary spines of the pygidium. These differences also apply to *P. llandowrorensis* Price, 1980 from the Ashgill of Wales, which also has the field of the fixed cheek a little broader than in the present *P.* aff. *caractaci*. *P. bucculenta* McNamara, 1979 from the Ashgill of northern England and Norway (see Owen 1981: 70) has a much broader fixed cheek field than any of these species, and whilst there are three pairs of spines between the primary spines of the pygidium there is only one or possibly two pairs outside them.

Subfamily **MIRASPIDINAE** Richter & Richter, 1917

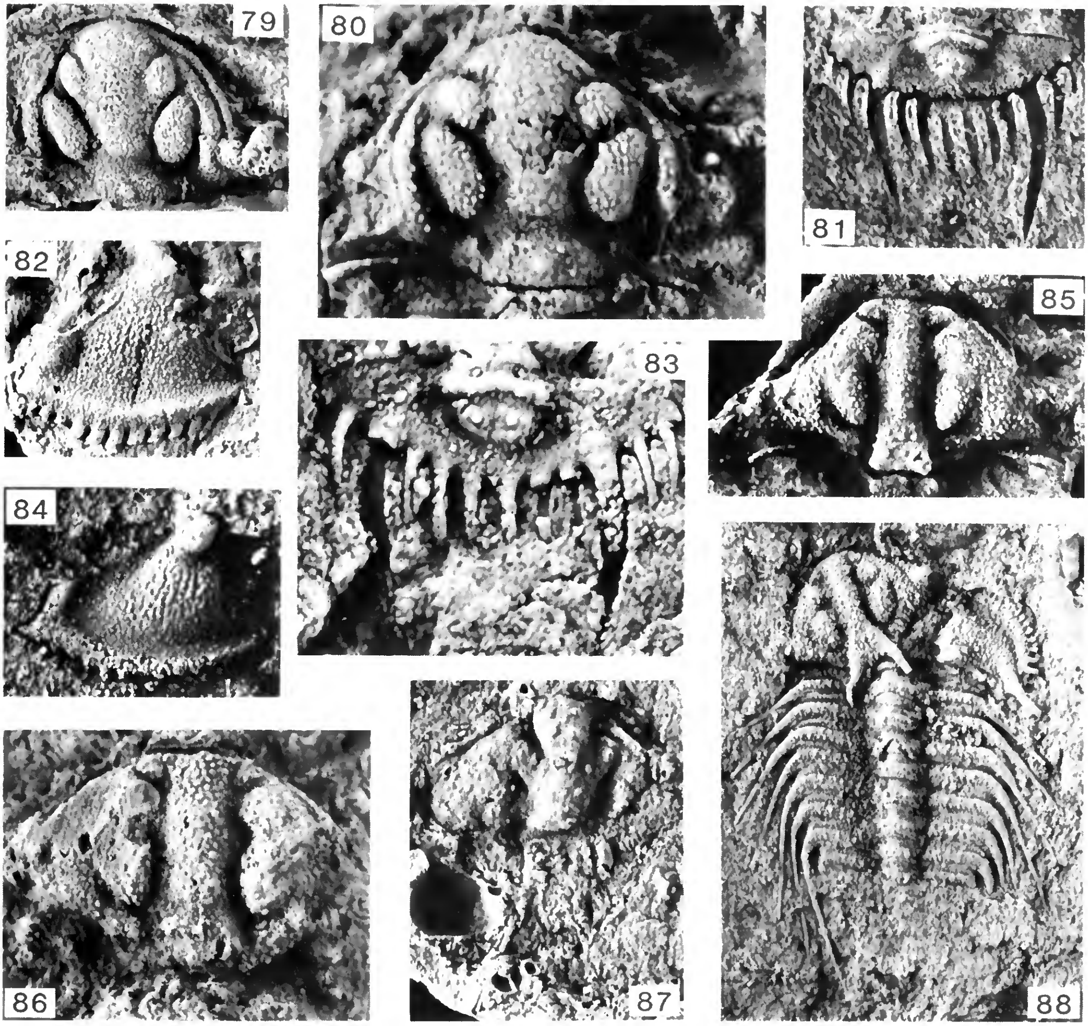
Genus ***MIRASPIS*** Richter & Richter, 1917

Type species. Original designation; *Odontopleura mira* Barrande, 1846: 57. From the Liteň Formation (Wenlock) near Beroun, Czechoslovakia.

Miraspis sp.
Figs 85–88

Material. Four cranidia and a slightly disarranged moult lacking the pygidium comprise 0·7% of the Raheen trilobite fauna.

Description. Length of cranidium (excluding occipital spines) slightly greater than half posterior width. Occipital ring narrow and long, occupying 25–30% of the sagittal glabellar length, tapering gently forwards and marked anteriorly by a very shallow furrow or even just a slight break in slope—the ring being more flat-lying than the preoccipital part of the glabella. No median occipital spine/tubercle is present, but a pair of long spines diverges rearwards and slightly upwards from the posterior edge of the occipital ring at about 60°. Preoccipital part of glabella almost circular in outline. Median lobe of glabella parallel-sided, defined by deep furrows as far forward as L3, and occupying 30% of the maximum width of the glabella, at the anterior ends of L1. L1 longitudinally oval, expanding (tr.) forwards over nearly three-quarters of their length. S1 diverge forwards at about 120°, dying out abaxially such that an extension of L1 is confluent with the subcircular L2. S2 diverge forwards at about 140°, broad and deep proximally, narrowing and becoming shallower abaxially. L3 undifferentiated anteriorly from the short (sag., exsag.) frontal lobe. Axial furrows well incised behind and along the posterior half of L1, where they curve abaxially forward from being transversely directed to being parallel. In front of this the glabella is differentiated from the fixed cheeks only by a break in slope. Field of fixed cheek almost triangular in outline, generally tapering forward but with a broad (exsag.) area extending behind L1 to the occipital ring. Posterior part of field steeply inclined from the posterior border. Posterior border ridge-like, directed gently abaxially in which direction it broadens a little, defined anteriorly by a deep, transversely-directed furrow. Base of eye stalk situated opposite the mid or anterior parts of L1. Details of stalk not known. Eye ridge defined adaxially by a shallow furrow directed from the base of the eye stalk to the anterolateral corner of the glabella at an angle to the sagittal line of about 40°. Anterior branch of facial suture defines the abaxial edge of this ridge. Details of posterior branch not known. External surface and internal mould of cranidium, excluding furrows, bear a dense coarse granulation.



Figs 79–84 *Primaspis* aff. *caractaci* (Salter). Fig. 79, It.19465, dorsal view of latex cast of cranidium, × 6½, sample N. Fig. 80, It.19466, dorsal view of internal mould of cranidium, × 11, sample 3. Fig. 81, It.17479, dorsal view of internal mould of pygidium, × 7, sample 3. Fig. 82, It.19467, oblique lateral view of latex cast of free cheek, × 6, sample 3. Fig. 83, It.17751, dorsal view of internal mould of pygidium, × 13, sample 3. Fig. 84, It.19468, oblique lateral view of internal mould of free cheek, × 6, sample N. Raheen Formation. See p. 115.

Figs 85–88 *Miraspis* sp. Fig. 85, It.17450, dorsal view of internal mould of cranidium, × 4, sample 3. Fig. 86, It.19469, dorsal view of internal mould of incomplete cranidium, × 8, sample 3. Fig. 87, It.19470, dorsal view of latex cast of incomplete cranidium showing long occipital spine, × 6, sample N. Fig. 88, It.17448, dorsal view of latex cast of slightly disarranged moult, lacking pygidium, × 4, sample 3. Raheen Formation. See p. 116.

Free cheek triangular in outline. Inner part of field steeply declined from the eye stalk but flattening out and becoming concave laterally and anteriorly adjacent to the weakly swollen border. Border bears at least 16 short, evenly-spaced spines. The main librigenal spine, of unknown length, is situated some distance behind the smaller spines and is an extension of a distinct swelling on the posterior part of the field. The adaxial part of the spine-base is abutted by a narrow posterior sutural ridge. External surface of free cheek densely covered by coarse granules.

Hypostoma not known.

Thorax of at least eight segments, tapering gently rearwards, known from a single specimen which lacks a pygidium. Axis strongly convex (tr.), occupying a quarter or less of the width of each segment. Axial furrow no more than a break in slope. Pleurae flat-lying, transversely directed. Principal pleural ridge (see Bruton 1966: 3–4 for definition of this and related terms) strongly swollen (exsag.) on anterior segments, progressively a little less so posteriorly; transversely directed except at distal extremity where it turns sharply rearwards. Long slender principal pleural spine directed abaxially rearwards at 60° to the sagittal line on the first segment and adaxially rearwards at 20° on the 7th (details of 8th not known). The orientation of the spines on the intervening segments form a gradation between these directions. Anterior accessory area bearing a well-developed ridge on the anterior segments; this is much less prominent posteriorly along the thorax. Posterior accessory area narrow (exsag.), poorly differentiated from the principal pleural ridge. An anterior pleural spine is visible on the first segment but this part of the segment is not preserved in the rest of the thorax. External surface of axis and pleural ridges densely covered in coarse granules. Posterior accessory areas and proximal parts of spines are more finely granular. Granulation on internal mould much more subdued.

Pygidium not known.

Discussion. The present material is described under open nomenclature pending the revision of *Miraspis jamesii* (Salter, 1853) from the Tramore Limestone. Salter's species was based on an articulated thorax and pygidium originally included in *Whittingtonia bispinosa* (M'Coy 1846), the lectotype of which is a cephalon from the Chair of Kildare Limestone (Ashgill) of Co. Kildare (see Warburg 1925: 251; Bruton 1966: 27; Dean 1974: 94).

The absence of a median occipital protruberance and the weakly incised occipital furrow distinguish the Raheen form from *M. ceryx* Whittington & Bohlin, 1958, *M. solbergensis* Bruton, 1966 and *M. cornuta* (Beyrich, 1846) from the Ordovician of Sweden, and suggest an affinity to *M.* sp. of Owen & Romano (*in* Harper *et al.* 1984). This last form is from the upper Ordovician Clashford House Formation and although incompletely known, its cranidium appears to differ in having a broader (tr.) median glabellar lobe and a more circular L1.

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Miscellanea I

Contents

A new *Stramentum* (Cirripedia) from the Lower Turonian of Nigeria

J. S. H. Collins

63 Oakhurst Grove, East Dulwich, London SE22 9AH

Synopsis

A new species of pedunculate cirripede, *Stramentum inconstans*, is described from the Lower Turonian of Lokpanta, south-eastern Nigeria, and comparisons are made with allied species. It represents the second member of the genus to be described from the continent of Africa and considerably extends the known range of the genus southwards.

Introduction

As defined by Withers (1935), the Stramentidae comprised the genera *Loriculina* Dames, 1885, *Stramentum* Logan, 1897 and *Squama* Logan, 1897. Both Withers (1935) and Hattin (1977) were of the opinion that *Squama* was founded on somewhat questionable material, now lost, and Hattin (1977), in his intensive study of the family, concluded that this genus 'is fiction, and that Logan was dealing only with some incomplete, poorly preserved specimens of *Stramentum*'. Hattin (1977) also redefined the generic status of both *Stramentum* and *Loriculina.*

The cirripedes recently discovered by Dr P. M. P. Zaborski (formerly of the University of Ilorin, Nigeria) in the Eze-Aku Formation of the Lower Turonian at Lokpanta, south-eastern Nigeria, meet the requirements of the genus *Stramentum* as now defined. The new species represents the second member of the genus to be described from the African continent and considerably extends the geographical range of the family southwards.

Of the nine species of *Stramentum* hitherto recognized (Hattin 1977), the earliest geologically, *S. saadensis* Davadie & Emberger 1954 (described from incomplete specimens from Libya), *S. texanum* (Withers 1945) and *S. syriacum* (Dames 1885) are from the Albian. *S. moorei* Hattin 1977 and *S. pulchellum* (G. B. Sowerby, jr 1843) are known from the Cenomanian and the latter ranges into the Turonian. Also of Turonian age are *S. canadensis* (Whiteaves 1889) and *S. elegans* Hattin 1977. The remaining species, *S. expansum* (Withers 1935) and *S. haworthi* (Williston 1897) are both from the Senonian.

Stratigraphy

At the type locality, the Eze-Aku River, near Ake-Eze, eastern Nigeria, the Eze-Aku Shale of Simpson (1955) consists of some 100 m of hard grey to black shales and siltstones with local facies changes to sandstones or silty shale. On the evidence of numerous vascoceratid ammonites Reyment (1965) considered this deposit to be of Turonian age. The ammonites probably floated into the area of deposition as dead shells, for the accompanying fauna which includes bivalves, gastropods, echinoids and fish teeth indicates a shallow water deposit.

Kogbe (1976) cast some doubt on Reyment's (1965) opinion that there was a connection between the Gulf of Guinea and the Mediterranean Sea during lowermost Turonian times, by saying that there was no definite evidence from the Sahara and North Africa to support it. As remarked below, p. 130, *S. inconstans* sp. nov. has affinities to the Cenomanian–Turonian species *S. pulchellum*, described from southern England, Ireland and Czechoslovakia, and it seems probable that the new species developed from that stock migrating southwards, rather than from the earlier *S. saardensis.*

Preservation and Substrates

The substrates of the specimens here examined consist of three pieces of fragmentary inner casts of acanthoceratid ammonites. Two of these pieces have cirripedes on both sides, indicating that the pieces themselves were lodged in a more or less upright position. In all but one instance the cirripedes, of which three or four distinct generations are present, are orientated in the same direction—whether on the 'left' or 'right' side of the substrate—presumably aligned so as to obtain best advantage of the currents regulating food supply.

Evidently the colonies were rapidly overwhelmed by sediment, for comparatively little disturbance of the valves has occurred. Indeed, so complete are the specimens that the description is impaired to some extent by the absence of isolated valves which would show the inner surface characters. There are one or two somewhat dispersed groups of plates and in one instance a capitulum has been sheared and displaced several mm from an otherwise undisturbed peduncle. The holotype and one other specimen have suffered the loss of peduncular plates in the median (i.e. upper lateral) column; in the holotype three plates beneath the first (fully grown) plate are missing and in In.62056 three plates are missing below the third plate and the previous three plates are compacted. That these losses were early is indicated by partial infilling of the resultant cavities, but no reason for them can yet be given.

Other *Stramentum* species attached to ammonites have been reported by Withers (1935, 1945) and Davadie & Emberger (1954). Besides cephalopods Hattin (1982: 75–76) listed other substrates occupied by *S. haworthi* (often in association with a minute scalpellid cirripede, *Zeugmatolepas* sp.) which included such truly benthonic forms as *Inoceramus* (*Volviceramus*) *grandis* (Conrad), *I.* (*Platyceramus*) *platinus* Logan and, rarely, *Pseudoperna congesta* (Conrad), oysters and rudists. From this Hattin (1982) concluded that the cirripedes themselves had a benthonic existence, rather than the pseudo-pelagic one as suggested by Miller (1968), and that those attached to ammonites had settled only on empty shells lying on the sea floor.

Systematic descriptions

The skeletal nomenclature adopted in this work follows Hattin (1977). All the material is in the Department of Palaeontology, British Museum (Natural History).

Class **CIRRIPEDIA** Burmeister, 1834

Order **THORACICA** Darwin, 1851

Suborder **LEPADOMORPHA** Pilsbry, 1916

Family **STRAMENTIDAE** Withers, 1920

Genus ***STRAMENTUM*** Logan, 1897

1897 *Stramentum* Logan: 188.
1920 *Stramentum* Logan; Withers: 69.
1935 *Stramentum* Logan; Withers: 311 (q.v. for intermediate synonymy).
1977 *Stramentum* Logan; Hattin: 807.

Diagnosis. Stramentids having scutum with subapical, commonly subcentral umbo. Individual plates in peduncular column beneath upper latus markedly imbricated with plates of adjacent columns.

Type species. *Pollicipes haworthi* Williston, 1896, by subsequent designation of Withers, 1920.

Range. Albian to Senonian.

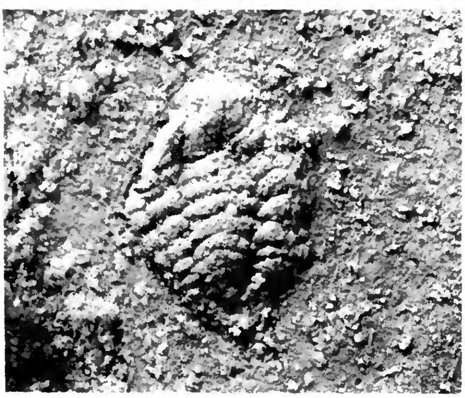
Stramentum inconstans sp. nov.
Figs 1–4

Diagnosis. A species of *Stramentum* with the scutum elongate-trapezoidal, the upper lateral margin and basal margin forming an angle of about 119°, and with umbo set between 0·75 to

1

2

5



3

4

Figs 1–4 *Stramentum inconstans* sp. nov. Lower Turonian, Eze-Aku Formation, Lokpanta, south-eastern Nigeria. Fig. 1, several complete individuals of various ages, showing right side uppermost, attached to an acanthoceratid ammonite. The holotype, In.62053, see also Fig. 4, is on the extreme left. × 1·5. Fig. 2, a group of partially displaced valves showing inner occludent edge of two right scuta, In.62059. × 1. Fig. 3, a very young complete individual, In.62054. × 5. Fig. 4, **holotype**, In.62053, showing peduncular plates missing from the upper lateral column, and the displaced edge of a valve against the carinal margin. × 3.

Fig. 5 *Stramentum pulchellum* (G. B. Sowerby jr). Turonian, *R. cuvieri* Zone; Cuxton, near Rochester, Kent. Holotype, individual with left side uppermost and carina and tergum missing. (G. B. Sowerby jr 1843; Withers 1935: pl. 41, fig. 4). BM(NH) 59150.

0·40 of distance from the apex to the rostral angle. Tergum with growth lines straight. The occludent margin is inflected in adults, less so in juveniles. The peduncular height ranges from about 3·10 to 3·80 times the height of the capitulum at the carinal margin, averaging 3·70. The peduncle is widest about midlength; the plates in the rostral column are about twice the width of those in the carinal column; the uppermost plates in the paired columns are more than twice as wide as high and those in the upper lateral column are variable in outline.

NAME. Alludes to the irregular size and form of the peduncle plates in the upper lateral column.

HOLOTYPE. A more or less complete skeleton, In.62053, on a fragment of an acanthoceratid ammonite (Figs 1, 4). Lower Turonian Eze Aku formation exposed in a road cutting on the Enugu–Port Harcourt express way at Lokpanta, south-eastern Nigeria.

MATERIAL. Besides the holotype there are 8 paratypes, In.62054–In.62061, of which In.62054-58 are on the same substrate as the holotype. In.62059-60 and In.62061 are on two similar but smaller ammonite fragments from the same horizon and locality.

DESCRIPTION. The height of the skeleton is approximately 1·5 times its greatest width. The junction of the capitulum to the peduncle is normally oblique from the carinal margin as far as the scutum, where it becomes straight to the rostral margin, the angle of incidence to the perpendicular height being about 34° in adults and somewhat less in juveniles. The peduncle is widest about midlength, and generally rather more boldly curved on the rostral side than on the carinal side where the bulge occurs further from the capitulum. The uppermost peduncular plate in the carinal lateral and upper lateral columns overlaps the base of the corresponding capitular valves, but as often as not the base of the scutum is left uncovered. The outer surface of the valves is generally glossy and devoid of longitudinal ridges; the normally inconspicuous growth lines are closely spaced apically, becoming less so towards the base; the leading edge of each ridge is slightly turned towards the apex. In some instances of more vigorous growth these ridges are broader and spaced much further apart, giving the surface a rippled appearance.

Scutum almost isosceles-triangular in juveniles, progressing to elongate-trapezoidal in adults, the maximum width generally a little less than half the height. The occludent margin is distinctly inclined towards the carinal side. The umbo is situated from 0·75 to 0·40 of the distance from the apex to the rostral angle and the umbonal angle ranges from about 109° to 123°, averaging 115°. There is sometimes a shallow excavation above the umbo, after which the occludent margin is nearly straight, or gently convex in more angular valves, to the apex; below the umbo it is gently convex. The rostral angle is rounded. The basilateral angle is not so rounded in adults, causing the basal margin to be straighter than in juveniles. The lateral margin is almost straight, but opposite the umbo it may be inflected obliquely towards the apex. No ridge is developed from the umbo to the basilateral angle; on the occludent side the surface is well rounded towards the margin, where only a narrow rostral slip can be determined; it then becomes flatter as far as the basilateral angle and then depressed to slightly excavate to the lateral margin, the excavation being limited above by a thickening divided by a thin groove along the upper occludent margin.

Part of the inner surface, revealed on In.62059 (Fig. 2), shows a trough (the occludent facet of Hattin, 1977), up to one third of the valve's width, extending parallel to the occludent margin; at the apex it is bounded for one third of its length by a conspicuous ridge which incurves and becomes obsolete basally. Within the trough the growth lines curve upwards from the occludent edge and become progressively more looped towards the base. Shortly below the apex on the lateral side there is a glimpse of the adductor muscle pit.

Rostrum. Seen only in lateral view, this reaches from about one quarter to one third the scutal height. It overlaps the basiscutal margin and extends about one third of the scutal width; its inner, scutal, margin is somewhat more strongly curved than its outer which, for the most part, follows the curve of the peduncle margin.

Upper latus nearly flat and triangular. The length of the basal margin is from 0·75 to 0·875 the length of the scutal margin; in height it reaches, or extends marginally beyond, the apex of the

scutum. The apical angle is between 49° and 61°, averaging 55°. The straight to gently convex scutal margin is slightly longer than the tergal margin, which is nearly straight. The basitergal angle is only a little more rounded than the basiscutal angle, neither conspicuously so. The growth lines follow the almost straight basal margin; along the tergal margin they turn abruptly towards the apex within the limited arc of the basitergal angle.

Tergum subtriangular in outline, transversely flattened from the carinal lateral margin to a 'line' (rarely developed as a rounded ridge, e.g. in In.62058) from apex to the occludent upper lateral angle, and then rounded to the occludent margin. The apex is acute and level with that of the carinal latus; the apical angle averages about 38°. The nearly straight carinal lateral margin is the longest and forms an angle of about 62° with the upper lateral margin which is nearly straight to gently convex. The occludent upper lateral angle may be rather narrowly or broadly rounded; this in turn affects the development of the occludent margin.

Carinal latus elongate triangular in outline, height about twice the basal width with the apical angle about 32°. Transversely it is nearly flat, becoming narrowly rounded towards the carinal margin. The tergolateral margin is the longest and is almost straight to slightly convex, the convex part being generally more noticeable apically. The nearly straight basal margin forms almost a right angle with the carinal margin. The growth lines follow the basal margin and turn up with the arc of the slightly rounded basal angle to form a narrow tergal slip; the growth lines on the tergal slip correspond with those on the tergum.

Carina. Seen only in lateral view, this reaches the apex of the tergum; it is bowed slightly inwards and tapers gradually from the apex to the basal margin. It is about five times as high as its basal depth.

In the holotype (In.62053) the carinal margin of the carinal latus on the obscured side projects fractionally and lies parallel to the outer margin of the carina. An apparently similar condition observed by Wyville Thomson (1858) in his *Loriculina macadami* (= *Stramentum pulchellum* (G. B. Sowerby jr)) led him to assume that the projecting capitular margin formed the inner edge of a carina naturally split longitudinally along the midline. Withers (1935) upheld this opinion and, furthermore, considered the presence of a split carina one of the important characters distinguishing *Stramentum* from *Loriculina*. This distinction, maintained by Newman *et al.* (1969), was dispelled by Hattin (1977) after a critical examination of Wyville Thomson's specimen revealed that the stramentid carina was typical of those of other lepadomorph barnacles.

Peduncle. Withers (1935: 302) presumed that the peduncle was comprised of five columns of overlapping plates on each side of the capitulum, the columns consisting of three rows of large plates lying under the scutum, upper latus and carinal latus respectively, with a smaller column along the carinal margin and another along the rostral margin. The two smaller columns were said to be in free apposition to the adjacent larger columns. From a study of peduncles belonging to several North American species of *Stramentum*, Hattin (1977) has conclusively demonstrated that the 'paired marginal columns', as formerly considered, consist only of a single column and that 'the stramentid peduncle consists of a single column of peduncular plates beneath each capitular plate and extends to the base of the capitulum'.

In the present species there is normally one more plate at the summit of the peduncle on the carinal and carinal lateral columns than on the rostral and scutal columns. The plates in the rostral and carinal columns are seen only in lateral view and those in the rostral column are about twice the width of those in the carinal column. Uppermost plates in the paired columns are three to four times as wide as high. The uppermost plates in the rostral column are about as wide as high with the rounded apex markedly overlapping the base of the plate above; in juveniles the plates are more quadrate and there is less overlap at the apex. The produced lower scutal angle is overlapped by the scutal plate of the preceding whorl.

The uppermost carinal plates are almost quadrangular, slightly higher than wide and a little less than half as wide as the corresponding plates in the adjacent column. They are slightly

convex on the outer margin and correspondingly concave on the inner margin where the basal angle is very slightly produced.

Of the paired columns the scutal plates are broadly trapezoidal, about twice as wide as high and rather more truncate on the rostral side; on the upper lateral side they are produced to a spur which overlaps the adjacent plate in the upper lateral column.

The upper lateral column plates are widest and subject to greatest variation according to their position relative to the curvature of the peduncle. At their widest the plates are four to five times as wide as high and about twice the width of those adjacent in the carinal column. The upper margin of the basal plates is very rounded to arcuate; it flattens as the width increases, becoming almost undulate and rather more attenuated on the carinal side. The narrower plates just below the capitulum are somewhat higher, have almost straight upper margins and are only a little wider than those on either side.

Plates in the uppermost whorls of the carinal lateral column are trapezoidal, with the lower lateral angle slightly produced; this angle decreases rapidly and the baseline increases correspondingly to accommodate the greater curve on the carinal side of the peduncle.

Discussion. In general appearance *Stramentum inconstans* most closely resembles *S. pulchellum* (G. B. Sowerby jr), but the latter differs in having a more smoothly rounded occludent margin and the scutal umbo is placed further from the apex; also the plates in the paired peduncular columns are more nearly equal in width, while those in the upper lateral column are altogether straighter and more regularly developed. Much the same can be said of the Senonian *S. haworthi* (Williston), but in this species the scutum is quadrangular, the carinal latus is less elongate, i.e. wider in proportion to length, and the upper lateral plates are, if anything, rather narrower than those adjacent.

S. elegans Hattin and *S. canadensis* (Whiteaves) have a longer capitulum in relation to overall length and the widest part of the peduncle occurs adjacent to the capitulum; the junction itself is more or less continuously oblique, not straightened below the scutum as in *S. inconstans*; and the scutum is distinctly arcuate at the umbo causing a much sharper inflexion to the occludent margin. *S. expansum* (Withers) is known by a single scutum which differs in the more central position of the umbo, and in the basilateral and rostral angles being almost right angles.

The capitulum of *S. saardensis* is poorly preserved, but according to Davadie & Emberger (1954) it occupied one fifth of the length of the skeleton. The widest part of the peduncle appears to be a little anterior to midlength and although the lower plates of the upper lateral column have a convex upper margin they quickly flatten; compared to those of *S. inconstans* they are higher than wide, more nearly equal in width to those in the adjacent columns and each plate is not nearly so tapered at the lateral angles.

The terga of *S. texanum* (Withers), *S. syriacum* (Dames) and *S. moorei* Hattin all have V-shaped growth lines, and by this character are immediately distinguishable from that of *S. inconstans* in which the growth lines are parallel to the basal margin. Should better preserved specimens of *S. saardensis* show it to have terga with similar V-shaped growth lines, then that species would display a more direct relationship with *S. syriacum* to the east and *S. texanum* (and the later *S. moorei*) to the west.

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Naefia (Coleoidea) from the late Cretaceous of southern India

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Synopsis

The coleoid *Naefia*, previously known only from Chile, is described from the late Cretaceous Ariyalur Group of Pondicherry, southern India. Two of the specimens described each possess a well-preserved conotheca from which the form of the pro-ostracum is deduced.

Introduction

The enigmatic coleoid *Naefia neogaeia* Wetzel was first described by Wetzel (1930) from the Quiriquina Formation (Campanian–Maastrichtian) of the island of Quiriquina, Chile. He based his description on two small phragmocones that differed from true belemnites by their acute apical angle and unusual siphuncle. Jeletzky (1966) later recognized its affinities with *Groenlandibelus rozenkranzi* (Birkelund), a late Cretaceous sepiid, and included both in his new family Groenlandibelidae. *Naefia* has not been recognized from anywhere outside Chile.

In the collections of the British Museum (Natural History) are three phragmocones from the Campanian to Maastrichtian Ariyalur Group of Pondicherry, southern India, which resemble both *Naefia* and *Groenlandibelus*. The phragmocones possess many of the features of *Naefia*, and are probably congeneric with it. The purpose of this paper is to describe in detail the first specimens of *Naefia* to be found outside Chile, and to make some comments on the shell structure of this genus.

The following abbreviations have been used: BMNH, British Museum (Natural History), specimen numbers prefixed by C; GPIK, Geologisches und Paläontologisches Institut, Kiel; MMK, Mineralogical Museum, Copenhagen; Dlmax, maximum lateral diameter; Dvmax, maximum dorsoventral diameter; Dlmin, minimum lateral diameter; Dvmin, minimum dorsoventral diameter.

Systematic descriptions

Subclass **COLEOIDEA** Bather, 1888

Order **?SEPIIDA** Zittel, 1895

Family **GROENLANDIBELIDAE** Jeletzky, 1966

TYPE GENUS. *Groenlandibelus* Jeletzky, 1966.

DISCUSSION. Jeletzky (1966) erected this family for those coleoids possessing narrow belemnite-like phragmocones, reduced rostra, oblique sutures, a wide siphuncle, and a caecum and prosiphon in their protoconchs. On this evidence he considered the family an early specialized member of the Sepiida, other members of which have similar phragmocones. However, Donovan (1977) has recently questioned the validity of this assignment and considered the Groenlandibelidae, the genus *Spirula*, and similar forms, separate from the Sepiida. Reitner & Engeser (1982) went further, placing the Groenlandibelidae and *Spirula* in a separate order, the Spirulida, mainly on the form of their protoconchs. Unfortunately, the specimens described below are incomplete, and no further light can be shed on the problem until more examples are found complete with their protoconchs.

Bull. Br. Mus. nat. Hist. (Geol.) **40** (4): 133–139 Issued 27 November, 1986

Genus *NAEFIA* Wetzel, 1930

TYPE SPECIES. *Naefia neogaeia* Wetzel, 1930, by original designation.

DIAGNOSIS. Groenlandibelidae characterized by a very narrow phragmocone (5·5–15°). Rostrum apparently much reduced or absent. Pro-ostracum spatulate, *Chondroteuthis*-like, with median keel and ridged asymptotes.

RANGE. Campanian–Maastrichtian of Chile, southern India and possibly the Antarctic Peninsula.

DISCUSSION. The form and affinities of *Naefia* have been discussed by Jeletzky (1966), and more recently by Biró-Bagóczky (1982) and Stinnesbeck (1986). Jeletzky (1966) re-examined the type specimens of *Naefia neogaeia* (GPIK 121a, b) and deemed them to be close to *Groenlandibelus rozenkranzi* (Birkelund) (holotype MMK MGUH.7758; see Birkelund 1956), uniting them in his new family Groenlandibelidae.

***Naefia* aff. *neogaeia* Wetzel, 1930**
Figs 1–4

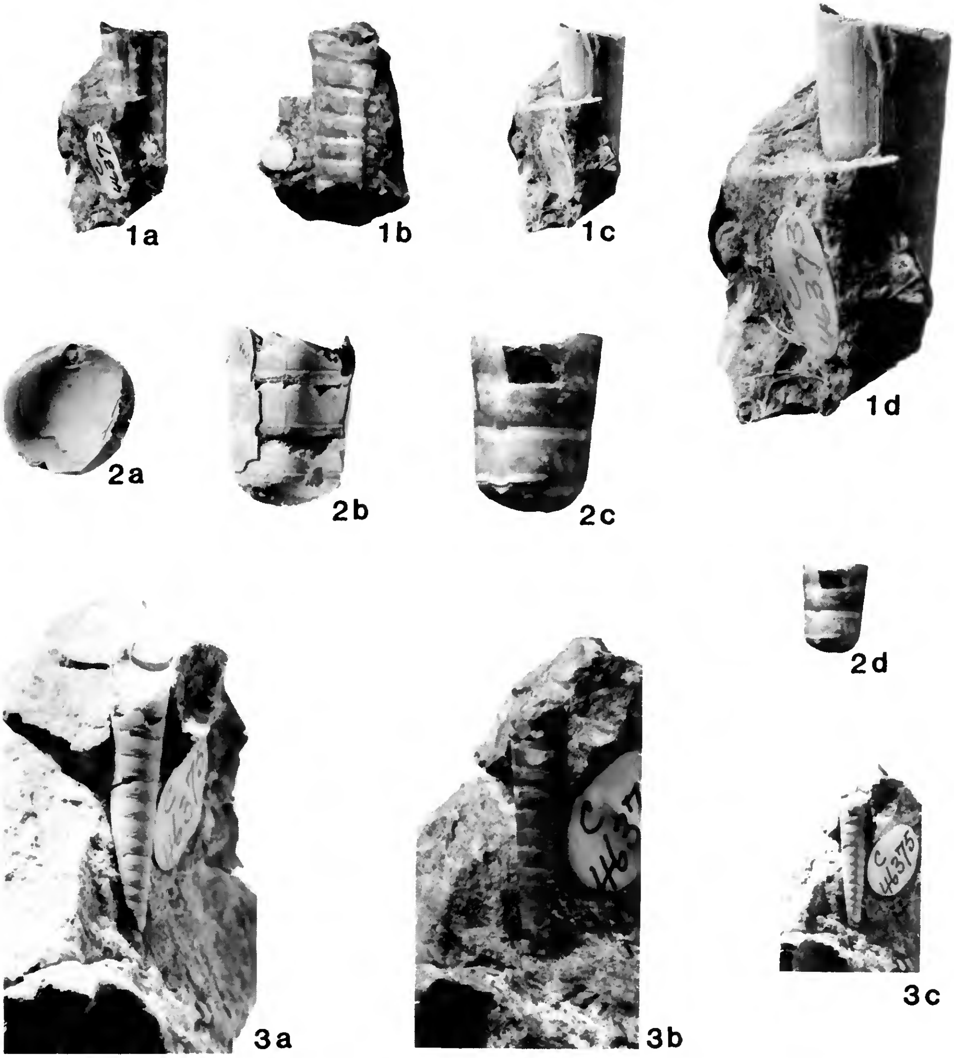
v 1846 *Belemnites* Forbes: 118; pl. 9, figs 4a, b (*non* fig. 3).
aff. v 1930 *Naefia neogaeia* Wetzel: 92; pl. XIV, fig. 3.
aff. 1982 *Naefia neogaeia* Wetzel; Biró-Bagóczky: A20; pl. 1, figs 1–5.
aff. 1986 *Naefia neogaeia* Wetzel; Stinnesbeck: 209; pl. 6, figs 6–7.

MATERIAL. Three phragmocones (BMNH C.46373-5) from the Campanian to Maastrichtian Ariyalur Group (Mettuveli–Valudayur formations), Pondicherry, southern India.

DESCRIPTION. *Naefia* aff. *neogaeia* is a small to medium-sized regular orthoconic phragmocone, with an apical angle of 5·5–8·5°, and apparently without a rostrum. The camerae are relatively high, the height to diameter ratio being 0·30–0·45. The septal sutures are oblique, and each possesses a ventral lobe. Details of the siphuncle are limited, but the connecting rings appear to be expanded adorally in the centre of the camerae. The pro-ostracum is *Chondroteuthis*-like, with a narrow spatulate form, a relatively wide median field, ridged median asymptotes and narrow hyperbolar zones.

Specimen C.46373 (original of Forbes 1846: pl. 9, fig. 4a) (Figs 1a–d, 4). This specimen is the largest of the three (maximum preserved length 24.5 mm), and consists of an orthoconic phragmocone with seven camerae preserved, although with apex and aperture missing. The maximum diameters of the shell are: 9·35 mm (Dlmax) and 9·80 mm (Dvmax), while the minimum diameters are: 6·25 mm (Dlmin) and 6·80 mm (Dvmin). The phragmocone has a regular undeflected axis and an apical angle of 8·5°. In cross section the phragmocone is slightly compressed. The height of the apical-most preserved camera is 3·05 mm, while that of the oral-most camera is 3·60 mm. The septal sutures are oblique to the long axis, and a ventral lobe is seen where the venter is exposed. The siphuncle is difficult to observe in this specimen. The dorsal conotheca is well preserved, and bears a median field with a median keel, ridged median asymptotes and narrow hyperbolar zones (see discussion below). However, it is not clear in hand specimen how many layers comprise the conotheca, although it appears to be more than one (cf. Jeletzky 1966).

Specimen C.46374 (original of Forbes 1846: pl. 9, fig 4b) (Figs 2a–d). This specimen is also an orthoconic phragmocone (maximum preserved length 11·80 mm), but with only three camerae (from the mid-region) preserved. The maximum diameters are: 8·45 mm (Dlmax) and 8·75 mm (Dvmax), while the minimum diameters are: 7·50 mm (Dlmin) and 7·65 mm (Dvmin). This phragmocone is generally similar to the last, with an undeflected long axis, an apical angle of 8° and a slightly compressed cross section. The height of the apical-most preserved camera is 3·30 mm, while that of the oral-most camera is 3·95 mm. The sutures are less oblique in this specimen than in the last, but again, a ventral lobe is developed. The siphuncle is just visible beneath the conotheca, and it is evidently marginal. Its actual form is difficult to determine in hand specimen, but the ?connecting rings appear to expand adorally. The width of the siph-



Figs 1–3 *Naefia* aff. *neogaeia* Wetzel. Ariyalur Group, Campanian–Maastrichtian, Pondicherry, southern India. Fig. 1, C.46373. 1a, dorsum, uncoated, × 1; 1b, right lateral view showing oblique septa (venter to right), uncoated, × 1; 1c, dorsum, coated, × 1; 1d, same view showing detail of the pro-ostracum, coated, × 2. Fig. 2, C.46374. 2a, oral-most septum showing ventrally-placed siphuncle, coated, × 2; 2b, dorsum showing median keel, coated, × 2; 2c, oblique ventral view (displaced to the left) showing faint outline of the siphuncle through the conotheca, uncoated, × 2; 2d, same view, uncoated, × 1. Fig. 3, C.46375. 3a, right lateral view showing oblique septa (venter to right), coated, × 2; 3b, oblique ventral view (displaced to the right), showing the ventral lobes, uncoated, × 2; 3c, same view, coated, × 1.

uncle is 1·50 mm where it is exposed on the lower surface of the apical-most septum. The conotheca is well preserved on the venter, but less so on the dorsum. However, enough is preserved to enable one to distinguish a median keel similar to that seen in the median field of the first specimen.

Specimen C.46375 (Figs 3a–c). This is a small (preserved length 17·35 mm) orthoconic phragmocone with 14 camerae, but without the apex or aperture preserved. The shell is slender and fragile, and is partly embedded in a matrix of bioclastic limestone. The following diameters

were obtained: 4·25 mm (Dvmax); 1·95 mm (Dlmin), giving an indication of its small size. This phragmocone, like those described above, is regular in form, with a straight long axis, and an apical angle of 5·5°. It is slightly compressed in cross section. The height of the apical-most camera is 0·75 mm while that of its oral-most camera is 1·25 mm. The protoconch is not preserved. The septal sutures are notably oblique, and a ventral lobe is very clearly displayed. The siphuncle is visible in the spar-filled camerae, and is marginal, close to the venter. Although again difficult to confirm in hand specimen, the connecting rings appear inflated adorally in the centre of the camerae. Unfortunately no details of the form of the septal necks can be determined. There are no traces of conotheca preserved with this specimen.

Form of the pro-ostracum. The well-preserved conothecae of C.46373–4 enable a reasonably accurate picture of the pro-ostracum of this species to be drawn. It possesses a relatively broad median field (in comparison with that of *Groenlandibelus*, see below) in the centre of which is a median keel. The median keel is itself divided by a sulcus running down its centre (Figs 1d, 4). The median field is bounded by median asymptotes which are unique in that each has a narrow ridge bounded by two sulci (Figs 1d, 4). The median asymptotes are bounded in turn by narrow hyperbolar zones, approximately one-third of the width of the median field. The parabolar growth lines of the median field are difficult to discern, and this makes estimation of the overall length of the pro-ostracum difficult. In form, the pro-ostracum described resembles that of the early Jurassic ?belemnoteuthid *Chondroteuthis* which is spatulate although much narrower than the 'typical' belemnite pro-ostracum (e.g. as figured by Crick, 1896). However, the pro-ostracum of *Chondroteuthis* attains a great length, up to three times that of the phragmocone (Jeletzky 1966), and it lacks the distinct ridged asymptotes seen in these specimens of *Naefia* (see Böde 1933) (Fig. 5). The morphological similarity of *Chondroteuthis* to the Groenlandibelidae has been noted elsewhere, although on different features (Jeletzky 1966), but it is unlikely that it is directly related to this family. Pro-ostraca of the Belemnitellidae (a late Cretaceous boreal belemnite family) also resemble that of *Naefia*, possessing a median keel bounded in

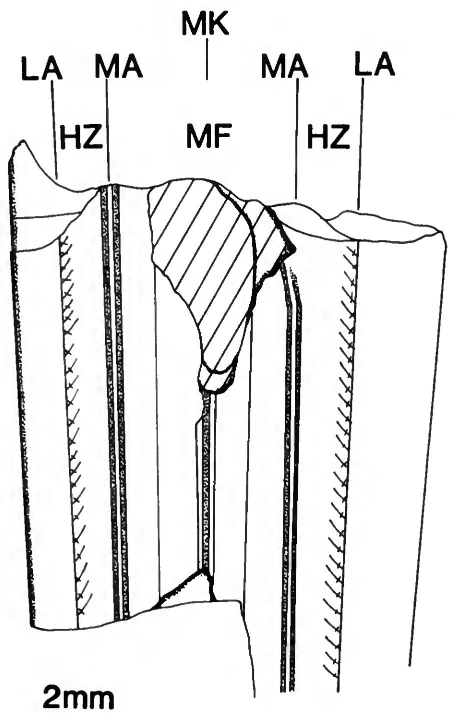


Fig. 4 Simplified camera-lucida drawing of the dorsal conotheca of specimen C.46373, showing the divided median keel and ridged median asymptotes. Cross-hatched area represents a detached conothecal fragment. Key to symbols: MK, median keel; MF, median field; MA, median asymptote; HZ, hyperbolar zone; LA, lateral asymptote.

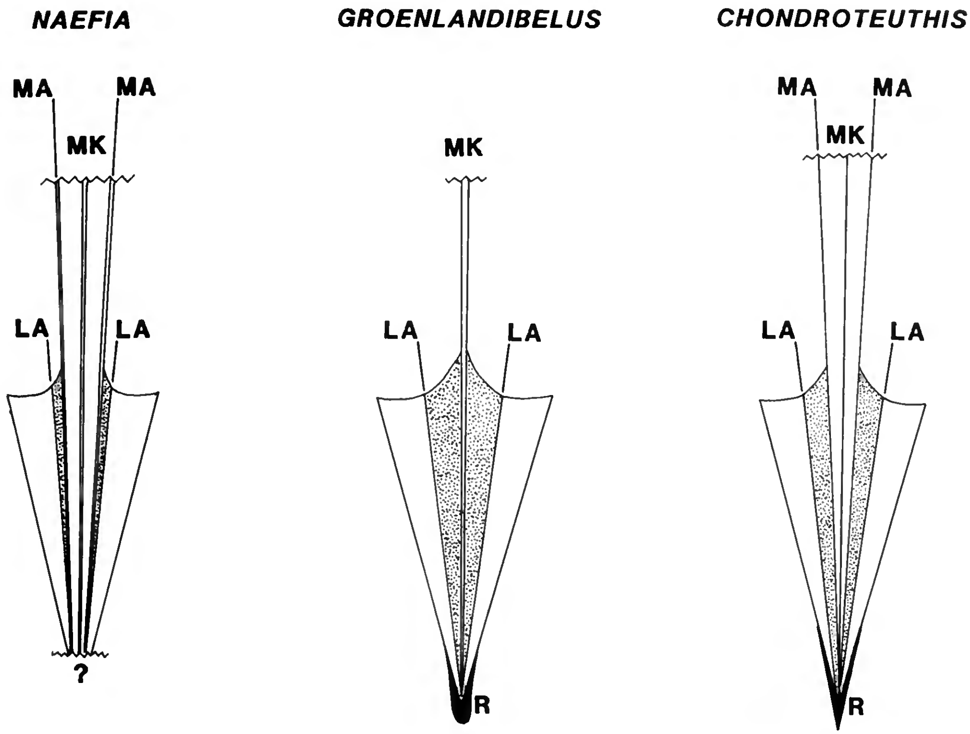


Fig. 5 Schematic comparison of the phragmocones and pro-ostraca of *Naefia*, *Groenlandibelus* and *Chondroteuthis*, not to scale. Stipple, hyperbolar zones; R, rostrum. Other symbols as given in Fig. 4.

some cases by ridges (Jeletzky 1966; Gustomesov 1980). However, belemnitellid phragmocones possess a ventral process not found in *Naefia*, and they have smooth median asymptotes and shorter camerae (Gustomesov 1980). The pro-ostracum of the other groenlandibelid, *Groenlandibelus*, is very different from that of *Naefia* (Fig. 5). Although both possess a median keel, *Groenlandibelus* lacks the additional median field that *Naefia* has, having instead very broad hyperbolar zones (Birkelund 1956; Jeletzky 1966). These broad zones are similar to those seen in the diplobelinid belemnites (Jeletzky 1966, 1981), which are also characterized by a median keel. Stinnesbeck (1986) has described a faint line on the dorsal conotheca of his Chilean *Naefia*, and this could be an incompletely preserved median keel as seen in the Indian specimen C.46374 (Fig. 2b). He also suggested that the conothecal growth lines of his specimens indicated the presence of a narrow pro-ostracum, which would appear to agree well with the Indian specimens.

The form of the pro-ostracum of the Indian *Naefia* does not necessarily preclude their assignment to the Groenlandibelidae (cf. Stinnesbeck 1986). Owing to the fragile nature of this structure (see Hewitt & Pinckney 1982), little is known about the variation in form of the pro-ostracum at genus and family level, although it is generally assumed that variation is small in taxa of low rank. Indeed, the only other sepiid pro-ostracum known, that of *Vasseuria* (Naef 1922: text-fig. 94e) is apparently spatulate (like *Naefia*), rather than thin and diplobelinid-like (as in *Groenlandibelus*).

DISCUSSION. The specimens described above are similar to *Naefia neogaeia* Wetzel and *Groenlandibelus rozenkranzi* (Birkelund) in the overall form of the phragmocone, the obliquity of its sutures and the presence of a ventral lobe. They apparently lack rostra (like *N. neogaeia*) and

differ from *G. rozenkranzi* in possessing a *Chondroteuthis*-like pro-ostracum. In addition, the Indian forms are rather larger than these species, with an extremely acute apical angle (5·5–8·5°, compared with 12·5–14° for *N. neogaeia* and 14–15° for *G. rozenkranzi*). Despite this, the broad morphological similarity between the Indian and Chilean forms would suggest they are congeneric. More certain attribution of the Indian forms to *Naefia neogaeia* depends on the definite recognition of the form of the pro-ostracum in topotypes of this species. The morphological differences between the Indian forms and *Groenlandibelus rozenkranzi* would appear to prevent their assignment to *Groenlandibelus* (see below).

In his original description of *Naefia neogaeia*, Wetzel (1930: 92) included some specimens described by Kilian & Reboul (1909) from Antarctica. Although stating their phragmocones were orthoconic, these authors gave no further morphological details, and this assignment must be treated with some doubt. Wetzel (1930) also referred to the Indian phragmocones figured by Forbes (1846). However, he excluded them from this species because they occurred with several fragments of belemnite rostra (see below).

AGE AND STRATIGRAPHICAL HORIZON. The molluscan fauna described by Forbes (1846) from Pondicherry has long been noted for its richness. The ammonites have been used as an example of a high diversity Maastrichtian fauna (Kennedy 1977: text-fig. 31). It includes a rich association of the genera *Brahmaites*, *Gaudryceras*, *Pachydiscus* and *Phylloptychoceras* (amongst others), indicating an age of Campanian to Maastrichtian (Kossmat 1897; Bhalla 1983; Henderson & McNamara 1985).

The belemnite phragmocones described above were found at Pondicherry with some poorly preserved fragments of rostra. The latter were tentatively assigned a new species name (*Belemnites? fibula*) by Forbes (1846) and consist of fragments of a compressed species, apparently possessing broad lateral depressions (Doyle 1985), which has been assigned to the early Cretaceous genus *Parahibolites*. Kossmat (1897: pl. VI, fig. 7) described more of these fragments and recognized that they were found in the ammonite-poor *Trigonarca* Beds (Mettuveli Formation, Maastrichtian). There is no direct evidence to link the belemnite phragmocones (treated entirely separately by Forbes, 1846) and the rostra, either morphologically or stratigraphically. The phragmocone of *Parahibolites* and its related forms (e.g. *Neohibolites*) is typically belemnitic, with an apical angle of 25–30° and a broad spatulate pro-ostracum, unlike that described above. In addition the matrix adhering to the rostra is a glauconitic sand, unlike the bioclastic shelly limestone enclosing the phragmocones. This limestone matrix is like that attached to the ammonites described by Forbes (1846), which are preserved in the British Museum (Natural History). The phragmocones may therefore have come from the ammonite-rich and stratigraphically lower Valudayur Beds (Valudayur Formation, Campanian–Maastrichtian).

Conclusions

1. *Naefia* differs from *Groenlandibelus* primarily on the form of its pro-ostracum, suggesting significant differences may exist in this feature at the generic level in other phragmocone-bearing coleoids.

2. The groenlandibelids were restricted to the Campanian–Maastrichtian time interval, *Groenlandibelus* in the boreal regions (only Greenland so far) and *Naefia* in the austral regions (South America, southern India and possibly Antarctica). Their phylogenetic relationships are as yet unclear.

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Neocrania n. gen., and a revision of Cretaceous–Recent brachiopod genera in the family Craniidae

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Synopsis

The new generic name *Neocrania*, type species *Patella anomala* Müller 1776, is proposed for the Recent and some Cenozoic inarticulate brachiopod species formerly included in the late Cretaceous genus *Crania* Retzius 1781. The history of the genus *Crania* is discussed, and new diagnoses and brief descriptions are given for *Crania* s.s., *Ancistrocrania*, *Craniscus*, *Isocrania*, *Danocrania*, *Valdiviathyris*, and *Neocrania*, the Cretaceous to Recent genera now contained in the family Craniidae Menke 1828. The new name *Neocrania reevei* is proposed for *Crania suessii* Reeve, non Bosquet, and lectotypes selected for this species and for *Craniscus tripartitus* (Münster).

Introduction

The punctate, calcareous-shelled inarticulate brachiopod genus *Crania*, which was established by Retzius (1781: 72), has undergone few major revisions in the past two centuries in comparison with other brachiopod genera described before 1800. Originally based on a late Cretaceous species from Sweden, *Crania brattensburgensis* Retzius 1781 (= *Anomia craniolaris* Linnaeus 1758), the genus expanded to include dozens of species ranging in age from Ordovician to Recent. Since the publication of Part H of the *Treatise on Invertebrate Paleontology* (Williams *et al.* 1965) most Palaeozoic species have been placed in separate genera, although *Crania* has still been widely used in a general sense for many species of Cretaceous to Recent age.

During a revision of living species included in the genus it became apparent that there were several major points of difference between living forms and the late Cretaceous type species *C. craniolaris*. These differences, which include shell structure, type of attachment, form of growth, and musculature, are sufficient to justify the establishment of a new genus, based on *Patella anomala* Müller, for many Recent and some Tertiary species formerly placed in *Crania*.

Historical survey of the Genus *Crania*

Twenty-three years after Linnaeus had described the first craniacean brachiopod, *Anomia craniolaris*, in the tenth edition of his *Systema Naturae* (1758), Retzius published his description of the new genus *Crania* (1781). He based the genus partly on the 'Brattensburg pennies' described by Stobaeus (1732) from the late Cretaceous of Sweden, with which he was familiar, and partly on a modern species from Philippine waters which he thought might be the same as *Anomia craniolaris*.

A general translation of Retzius' Latin diagnosis of *Crania* is as follows: 'Shell bivalved, subequilateral, subequivalved, orbicular. Hinge edentulous. Lower valve with three scars as pits intruding into the valve, two of which are hemispherical with their bases inserted within the hinge margin: the third situated in the centre is larger and subtriangular and surrounded by the

elevated margin. Upper valve with two prominent scars placed within the hinge margin, corresponding with the scars of the lower valve. The third scar does not correspond and is deep within the internal convexity situated beneath a pair of small oblique ridges'.

Retzius described two species, *Crania brattensburgensis*, within which he cited *A. craniolaris* Linnaeus, and *C. egnabergensis*, in which he included the non-binomial *Nummulus minor* Stobaeus. The localities for the former were the Recent seas of the Philippines (for the specimen which he had called *C. craniolaris*) and the Isle of Ivö, Balsberg, and Ignaberga, southern Sweden, for the fossil specimens. The chalk pit at Ignaberga was also the type locality for *C. egnabergensis*. Thus in proposing *Crania*, which like Linnaeus' species name *craniolaris* referred to the skull or face-like appearance of the ventral valve interior, Retzius included living as well as his more local late Cretaceous species in his concept of the genus.

In the early nineteenth century, Lamarck (1819) introduced alternative names for some previously described species of *Crania*. These names, which included *C. nummulus* for *Crania craniolaris* (Linnaeus 1758), and *C. striata* for *Crania egnabergensis* Retzius 1781, were followed by a number of later workers including Nilsson (1826), Hoeninghaus (1828), and Münster (*in* Goldfuss 1840), and were the source of a great deal of confusion which was compounded by apparent unawareness of Müller's (1776) name of *Patella anomala* for the common Recent north Atlantic species.

In his comparison of the principal classifications in use at the time, Schmidt (1818) recorded the 'type' of *Crania* as *Anomia craniolaris* as figured by Chemnitz (1785: fig. 687), who was redescribing Linnaeus' specimens. This has been taken, under ICZN Rules (1985: 133), as the valid assignment of the type species. Some of the best and most easily identifiable illustrations of craniacean brachiopods are those of Hoeninghaus (1828), who described thirteen living and fossil species. Some of these plates were used again by Münster (*in* Goldfuss 1840), when he described species of Jurassic to Recent *Crania*.

The first comprehensive account of the various Recent species of *Crania* was that of Reeve (1862), who described with clear illustrations the living species *Crania anomala* (Müller) from the north Atlantic, *C. turbinata* Poli from the Mediterranean, *C. rostrata* Hoeninghaus from west Africa, and a new species from Australia, *C. suessii* Reeve (but see *Neocrania*).

In 1871 Dall discussed *Crania* at length, providing extensive synonymies. He was, however, incorrect in writing (1871: 30) that the Recent specimen from the Philippines discussed by Retzius (1781) was probably the same species as that 'previously described by Müller (1776) under the name of *Patella anomala*', from Scandinavian seas. *Crania anomala* (Müller) is a locally common constituent of north Atlantic benthic faunas and has been studied anatomically and developmentally by, for instance, Blochmann (1892) and Rowell (1960). Dall himself much later described a new species from Philippines waters as *Crania philippinensis* (Dall 1920). Dall (1871) was, however, correct in demonstrating how Recent species names, such as *anomala*, were often confused by late eighteenth and nineteenth century authors with fossil species, mainly from the Cretaceous.

Between 1818 and 1885 numerous species of Cretaceous to Recent age were attributed to the genus *Crania* by many authors including Defrance 1818, Sowerby 1823, Nilsson 1826, 1827, Hoeninghaus 1828, Münster (*in* Goldfuss 1840), Hagenow 1842, d'Orbigny 1847, Davidson 1852, 1856, Bosquet 1854, 1859, and Lundgren 1885.

An early attempt to subdivide the genus *Crania* was made by Dall (1871) when he proposed a new genus *Craniscus* (type species *Crania tripartita* Münster 1840), and a new subgenus *Craniopsis* (= *Ancistrocrania* Dall 1877) (type species *Crania parisiensis* Defrance 1818). Two further subdivisions, designating *Crania egnabergensis* Retzius 1781 as type species of the new genus *Isocrania*, and *Crania tuberculata* Nilsson 1826 as the type of a new subgenus *Danocrania*, were carried out this century by Jaekel (1902) and Rosenkrantz (1964) respectively.

Unlike the subdivisions of most of the other broadly defined 'sack' genera of brachiopods, such as *Rhynchonella* and *Terebratula* which have long since been subdivided into more restricted genera, those separated off from *Crania* do not seem to have been generally accepted. For example, although *Ancistrocrania* and *Isocrania* have been in the literature for well over fifty years, they were not accepted by Carlsson (1958) in his revision of *Crania* from Sweden,

and were recognized only as subgenera by other revisers of this group including Rosenkrantz (1964) and Kruytzer (1969).

Further problems have arisen where a figured type species of one genus has been placed inadvertently in another. For example, Roger (*in* Piveteau 1952), although listing *Isocrania* as a full genus, named an excellent figure of the type species, *I. egnabergensis*, as *Crania* s.s. More recently, Cocks (*in* Murray 1985) figured the type of *Danocrania*, *D. tuberculata*, under the name *Ancistrocrania*.

Systematic descriptions

In this paper revised diagnoses, descriptions and figures of the type species are provided for the Cretaceous to Recent genera now included in the family Craniidae. Species we have inspected, and believe to be well authenticated, are assigned to the appropriate genera and marked in the species lists with an asterisk (*). Other species are assigned on the basis of the literature. All specimens figured are in the collections of the Department of Palaeontology, British Museum (Natural History), unless otherwise stated. Genera are described in chronological order.

Order **CRANIIDINA** Waagen 1885

Superfamily **CRANIACEA** Menke 1828

Family **CRANIIDAE** Menke 1828

DIAGNOSIS. Shell calcareous, punctate, puncta in dorsal valve branching in some Recent genera. Dorsal valve usually conical, ventral valve subconical or convex when free, conforming to shape of attachment surface when fixed.

Genus ***CRANIA*** Retzius (1781: 72)

DIAGNOSIS. Posteriorly-attached, posteriorly-directed muscle pits, with pseudointerarea in *C. antiqua*. No strongly developed dorsal muscle scars.

TYPE SPECIES. *Anomia craniolaris* Linnaeus (1758: 700), by subsequent designation of Schmidt (1818: 71). The lectotype, a ventral valve selected by Brunton & Cocks (*in* Brunton *et al.* 1967), a second ventral valve, and a dorsal valve, are in the collection of the Linnean Society, London, 183 A–C (numbered from Linnaeus, 1758). The type specimens were first figured by Chemnitz (1785: pl. 8, fig. 687a, b).

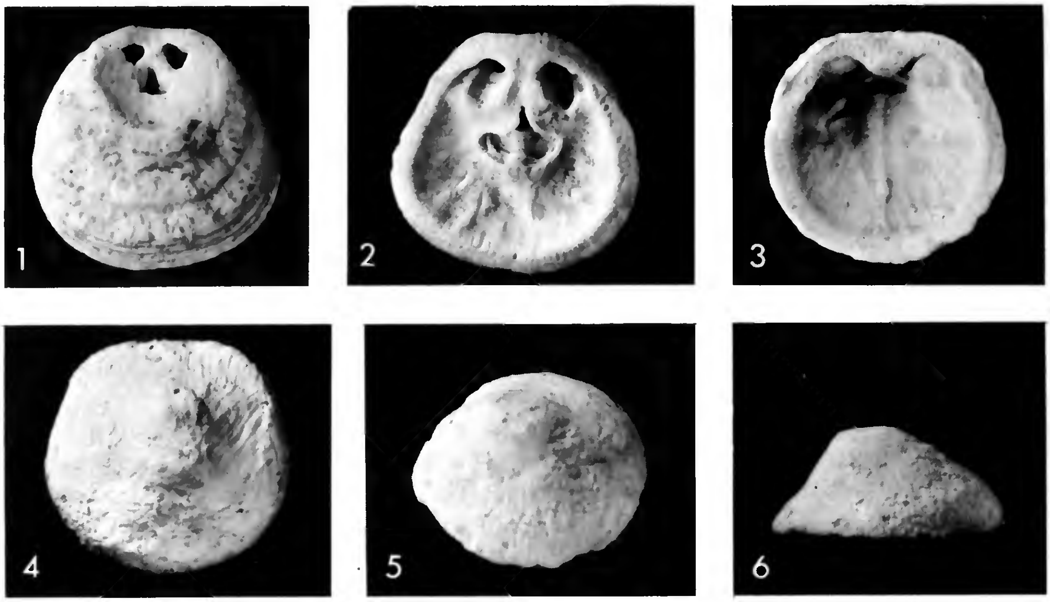
The type locality is Ivö (Ugnsmunnarna), Scania, Sweden. In both 1758 and 1767 Linnaeus described the locality of *A. craniolaris* as Ivö and Balsberg, Scania. There is no indication which locality yielded the three specimens in the Linnaean Collection so it would seem correct to designate the former as the type locality. The locality known to Linnaeus and Retzius as Ivö, 'a cliff section with natural caves' on Ivö Island in Lake Ivö, is now known as Ugnsmunnarna, *sensu* Christensen (1975). The locality now referred to as Ivö Klack was discovered in the latter part of the nineteenth century (W. K. Christensen, personal communication 1985). According to Lundegren (1934) and Christensen (1975) the Ivö localities are all of latest Lower Campanian age.

INCLUDED SPECIES. **Anomia craniolaris* Linnaeus 1758 (= *Crania brattensbergensis* Retzius 1781). Figs 1–6, 40–41.
**Crania antiqua* Defrance 1818. Figs 42–45.

GEOGRAPHICAL RANGE. Sweden, Denmark, France, Netherlands, Belgium, U.S.S.R.

STRATIGRAPHICAL RANGE. Upper Cretaceous, Campanian–Maastrichtian.

DESCRIPTION. Shell of medium size (maximum length 20 mm), subcircular in outline with maximum width towards shell anterior. Ventral valve attached only posteriorly, scar up to $\frac{1}{3}$ shell length. Mixoperipheral growth slight to well-developed, often producing a pseudo-



Figs 1–6 *Crania craniolaris* (Linnaeus). Lectotype and paralectotype from Ivö, Scania, of Lower Campanian age, in the collections of the Linnean Society of London. Specimens are numbered from Linnaeus, 1758. Figs 1, 2, lectotype, 183A, ventral valve exterior and interior respectively. Note medium-sized posterior attachment cicatrix, the perforations of the valve exterior by the posteriorly-directed muscle pits, and the 'face-like' appearance of the valve interior. × 3. See also Fig. 38. Figs 3–6, paralectotype, 183C, respectively interior, exterior, oblique and lateral views of dorsal valve. × 3. See also Figs 40–41.

interarea. Internally planar to concave with deeply incised muscle scars originating postero-medially, often perforating the valve externally (Figs 1, 2). Valve thickened with tuberculate marginal rim.

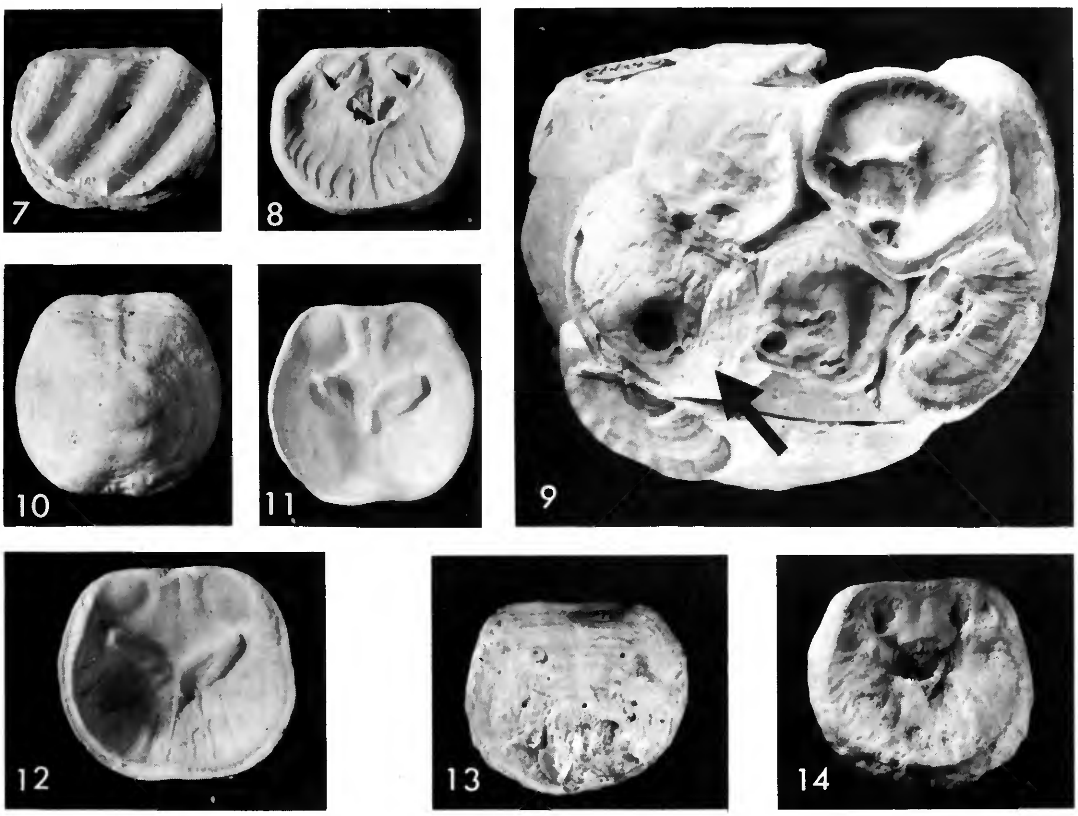
Dorsal valve with almost straight posterior margin and posteriorly directed umbo. Shell exterior smooth or with slightly pustulose ornament. Well-defined posterior muscle scars, in front of which there is a weak median ridge.

Genus *ANCISTROCRANIA* Dall (1877: 13)
(nom. nov. for *Cranopsis* Dall, 1871: 27, non *Cranopsis* Adams 1860)

DIAGNOSIS. Dorsal valve with two raised anterior adductor scars not united medially. Ventral valve attachment scar central to whole surface.

TYPE SPECIES. *Crania parisiensis* Defrance (1818: 313; not figured), by original designation. The type specimens probably no longer exist; according to Cleevely (1983), the Defrance fossil invertebrate collection in the Musée d'Histoire Naturelle, Caen, was destroyed in June, 1944. Kruytzer (1969) noted that the first illustration, which did not however show the diagnostic processes in the dorsal valve, was that of Cuvier & Brongniart (1822). The types were from Chalk of Campanian age at Meudon, near Paris (Diffre & Pomerol 1979).

INCLUDED SPECIES. **Crania parisiensis* Defrance 1818. Figs 7–9, 39.
C. abnormis Defrance 1818
C. nodulosa Hoeninghaus 1828
**C. comosa* Bosquet 1854
C. bredai Bosquet 1854
**C. davidsoni* Davidson 1856. Figs 10–14, 46–47.
C. mulleri Bosquet 1859



Figs 7–9 *Ancistrocrania parisiensis* (Defrance). Topotypes from the Campanian chalk of Meudon, France. Figs 7, 8, exterior and interior views of a ventral valve attached in life to an inoceramid shell. B53203, × 1. See also Fig. 39. Fig. 9, six specimens attached to an echinoid; note the nearly complete dorsal valve in life position on the arrowed individual. B5993, × 1·5 (figured by Davidson 1853: pl. 1, fig. 7).

Figs 10–14 *Ancistrocrania davidsoni* (Davidson). Figs 10–11, exterior and interior views of dorsal valve showing diagnostic raised processes on anterior muscle scars. Maastrichtian chalk, Ciply, Belgium. BD3354, × 1·5. Fig. 12, interior of second dorsal valve from Ciply. BD3355, × 1·5. Figs 13–14, exterior and interior views of an anteriorly attached ventral valve from Vetschau, near Aix-la-Chapelle, of Campanian age. Note the anteriorly-directed muscle pits. Davidson Collection. B5990, × 1. See also Figs 46–47.

**C. suessi* Bosquet 1859
C. quadrangularis Lundgren 1885
C. retzii Lundgren 1885
?*C. bromelli* Lundgren 1885
?*C. stobaei* Lundgren 1885
Craniscus hesperius Cooper 1955

Geographical range. France, Belgium, Netherlands, Sweden, England, North America.

Stratigraphical range. Upper Cretaceous, Senonian–Maastrichtian, (?Danian).

Description. Ventral valve medium- to large-sized with central to anterocentral initial attachment area and scar of variable size. Planar to concave or conical internally with much thickened shell. Muscle scars, especially anterior ones, deeply sunken in pits originating anteriorly. Slightly pustulose crest to submarginal rim, with smooth outward facing surfaces.

Dorsal valve relatively thin-shelled. Umbo slightly posterior of central with low ridge to mid-posterior margin. Internally with large posterior muscle scars. V-shaped ridges, bearing anterior adductor scars, widen posteriorly to form short, slender processes near posterior scars; a small median ridge extends anteriorly from their apex. Shell exterior smooth or with pustulose ornament.

REMARKS. Davidson (1856) figured a new species of *Crania* using a manuscript name of Bosquet three years before the latter's publication appeared, and thus inadvertently became the author of a species named after himself.

Genus *CRANISCUS* Dall (1871: 27)

DIAGNOSIS. Dorsal valve with three ridges joined medially.

TYPE SPECIES. *Crania tripartita* Münster (1840: 297), by original designation. The dorsal valve figured by Münster is here selected as **lectotype** (Figs 15, 16); it is housed in the Bavarian State Museum, Munich, number AS VII 171. (There are three paralectotypes). The lectotype was newly figured by Rowell (*in* Williams *et al.*, 1965: fig. 181.3a–c). It is from coral limestone of Jurassic (Lower Oxfordian) age (pebbles in a stream), near Thurnau, northern Bavaria, Germany (Barczyk 1968).

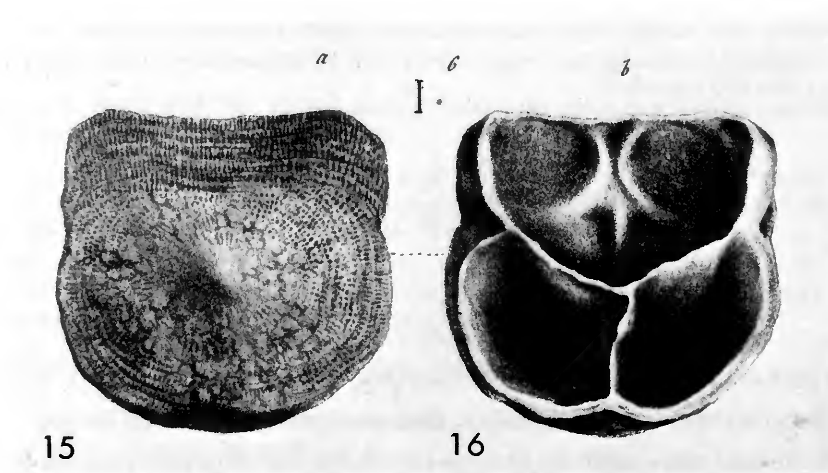
INCLUDED SPECIES. **Crania tripartita* Münster 1840. Figs 15–16.
**C. suevica* Quenstedt 1857
**C. japonica* Adams 1863. Figs 17–18.
C. quadrangularis Tate 1893 (*non* Lundgren 1885)
= *Ancistrocrania skeatsi* Allan 1940

Several other species from the Jurassic were placed in *Craniscus* by Rollier (1915–16) and Barczyk (1968). Nekvasilova (1982) has recently assigned a new species from the Lower Cretaceous of Czechoslovakia to this genus.

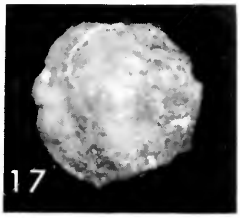
GEOGRAPHICAL RANGE. Europe, Australia, Japan, Indo-Pacific seas.

STRATIGRAPHICAL RANGE. Upper Jurassic–Recent.

DESCRIPTION. Small to medium-sized shell; ventral valve attached by entire surface. Dorsal valve relatively thin-shelled, weakly to strongly convex, margins of valves not thickened. Anterior adductor muscle scars variable, raised on ridges or platforms; united with a raised median myophore or short ridge which partially divides valves into three sections.



Figs 15–16 *Craniscus tripartitus* (Münster). Copy of the original illustration of the **lectotype** (herein selected) of the species, after Münster (*in* Goldfuss 1840: pl. CLXII, fig. 6a, b). The lectotype is a poorly preserved silicified specimen in the Bavarian State Museum, Munich, number AS VII 171. Note that its length is about 4·7 mm, and that most of the anterolateral margin of the shell appears to be broken or worn away.



Figs 17–18 *Craniscus japonicus* (Adams). Exterior and interior views of a dorsal valve of a small Recent specimen from Japan. Cuming Collection. ZB132, × 5.

REMARKS. In describing the new genus *Craniscus*, Dall (1871) noted that 'the differences between the genera *Crania* and *Craniscus* are fully as great as any existing between the acknowledged genera of the Terebratulidae'. His original diagnosis of *Craniscus* wrongly stated that it was the 'fixed' or ventral valve which was divided into three parts, but he subsequently corrected this (Dall 1877, 1920). In fact, although the type specimen displays three chambers in the dorsal valve interior separated by three vertical wall-like septa (Figs 15–16), few other specimens attributed to *Craniscus* show this feature. It is worth noting that the type locality is a stream-bed, and we suspect that the valve margins of the lectotype are broken or worn away. If so, then the dorsal valve ridges do not normally reach the valve margins. This is certainly true for specimens of the closely related *Craniscus suevica* of late Oxfordian age in the collections of the British Museum (Natural History).

Genus *ISOCRANIA* Jaekel (1902: 1062)

DIAGNOSIS. Strong radial ribbing on both valves, biconvex, small to no attachment scar.

TYPE SPECIES. *Crania egnabergensis* Retzius (1781: 75), by subsequent designation of Schuchert & LeVene (1929: 69). The type specimens are unknown (Surlyk 1973), but the locality is given as Ignaberga, Scania, southern Sweden. The age is Lower Campanian (Christensen 1975).

INCLUDED SPECIES. **Crania egnabergensis* Retzius 1781. Figs 19–22.
**C. costata* Sowerby 1823
C. barbata Hagenow 1842
**C. paucicostata* Bosquet 1859
**Isocrania faxensis* Nielsen 1911
I. posselti Rosenkrantz 1920

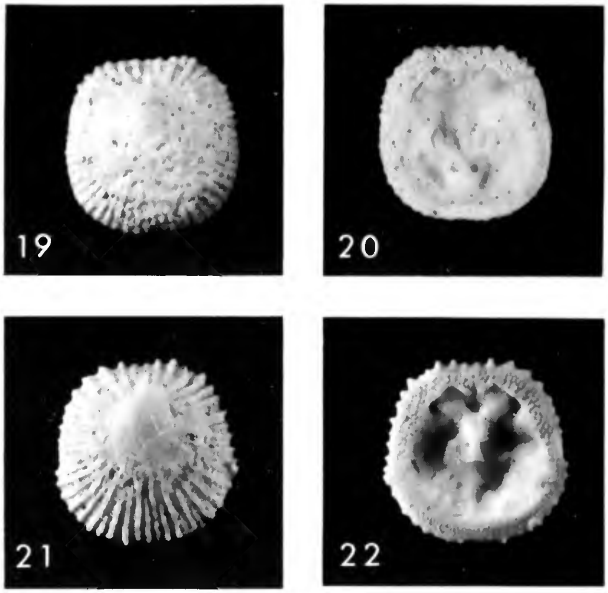
GEOGRAPHICAL RANGE. Sweden, Denmark, Netherlands, England, Africa, Asia.

STRATIGRAPHICAL RANGE. Upper Cretaceous–Lower Tertiary, Campanian–Danian.

DESCRIPTION. Small, biconvex shell with little or no ventral valve attachment, strongly costellate with additions by intercalation. Marginal rims flattened and papillose in both valves.

Ventral valve interior rounded with slightly raised posterior muscle scars. Anterior scars small, separated by a prominent short median ridge (nose).

Dorsal valve interior with slightly raised posterior scars and two pairs of anterior scars; one widely separated median pair and the other smaller pair set close together anteriorly.



Figs 19–22 *Isocrania egnabergensis* (Retzius). Both specimens are from Oretorp, 1 km south-east of Ignaberga, Sweden, of Campanian age. Figs 19–20, exterior and interior views of a dorsal valve. Note the extreme anterior position of the anterior muscle scars. BD3373, × 3. Figs 21–22, exterior and interior views of a ventral valve. BD3372, × 3.

Genus *VALDIVIATHYRIS* Helmcke (1940: 237 (23))

TYPE SPECIES. *Valdiviathyris quenstedti* Helmcke (1940), by original designation. Known by a single dorsal valve, specimen No. 198, Humboldt University, Berlin (Rowell 1962: 542). From Station 165, Deutschen Tiefsee Expedition 1899, near St Paul I., south Indian Ocean, in 672 m. Recent.

REMARKS. Rowell (1962) re-examined the single valve known for this genus, and concluded that it was a juvenile (length 2·5 mm, width 4·7 mm), and possibly related to *Ancistrocrania*. Until further specimens are found, the relationship of this species to other craniids is not determinable.

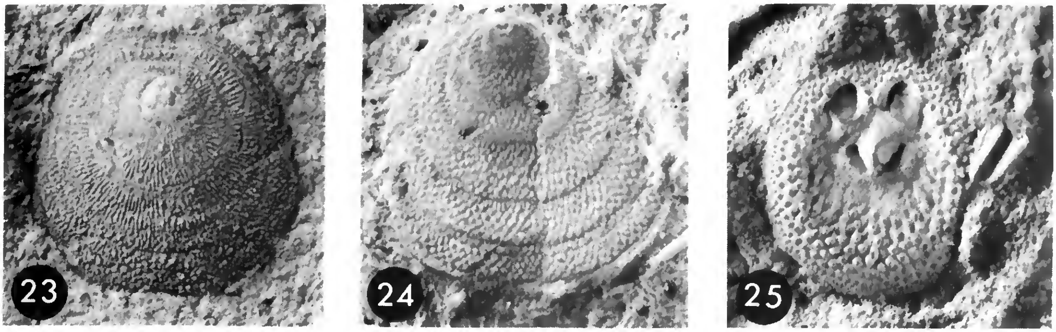
Genus *DANOCRANIA* Rosenkrantz (1964: 515)

SYNONYM. *Westalicrania* Cockbain (1967: 75; type species *W. allani* Cockbain, by original designation.

DIAGNOSIS. Exterior pustulose to spinose, ventral valve interior commonly tuberculate and muscle scars in shallow pits.

TYPE SPECIES. *Crania tuberculata* Nilsson (1826, emended 1827) (= *Craniolites brattenburgicus* Schlotheim 1820), by original designation. Nilsson's type material in Lund University Geological Institute cannot now be found (K. Lindholm, personal communication 1985). From Scania, southern Sweden; of Danian age.

INCLUDED SPECIES. **Crania tuberculata* Nilsson 1826 (emended 1827). Figs 23–28.
**C. spinulosa* Nilsson 1827. Figs 29–31.
**C. hagenowi* Davidson 1852
C. kressenbergensis Gümbel 1861
C. austriaca Traub 1938
C. geulhemensis Kruytzer & Meijer 1958
Danocrania polonica Rosenkrantz 1964
Westalicrania allani Cockbain 1967



Figs 23–25 *Danocrania tuberculata* (Nilsson). All specimens are from the Danian Saltholm Limestone, South Harbour, Copenhagen, presented by Dr A. Rosenkrantz. Fig. 23, finely spinose dorsal valve exterior. B80856, × 3. Fig. 24, slightly damaged ventral valve exterior. B80850, × 3. Fig. 25, highly tuberculate ventral valve interior. B80858, × 3. See also Figs 26–28.

GEOGRAPHICAL RANGE. Sweden, Denmark, Belgium, Netherlands, Austria, Ukraine, Crimea, Australia.

STRATIGRAPHICAL RANGE. Upper Cretaceous–Paleocene, Maastrichtian–Danian, (?Thanetian).

DESCRIPTION. Shell small to large, mostly thin-shelled. Shell exterior, especially on dorsal valve, pustulose to spinose with quincuncial/radial arrangement.

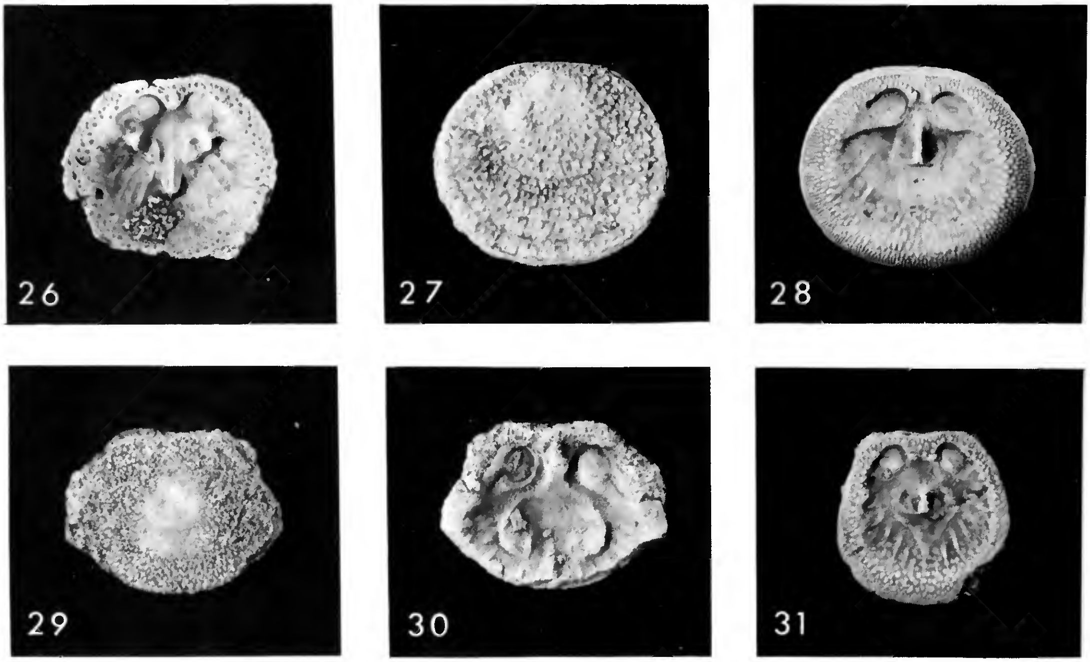
Ventral valve with small, posteriorly positioned attachment scars. May develop small pseudointerarea. Internally, a strongly tuberculate rim may form an extension between the well-defined posterior muscle scars, which may be raised. Anterior scars separated by a prominent short median ridge ('nose') with the rest of the 'face' being tuberculate to radially ridged.

Dorsal valve interior with flattened articulatory ridge between the posterior muscle scars. Anterior muscle scars broad, widely separated but converging anteriorly. Weak anteromedian ridge and slight radial ridging within the marginal rim.

REMARKS. In 1820 Schlotheim figured, poorly and without description, a new 'genus' and species of brachiopod, *Craniolites brattenburgicus*, from a limestone (possibly also a reworked limestone) at Copenhagen. He noted that it differed from other species found in Denmark and contrasted it with *Crania craniolaris* from southern Sweden. Several years later, Nilsson (1826, emended 1827) described a number of new brachiopod species, including *Crania tuberculata* from Scania. From the time of the first revision of Schlotheim's specimens by Hoeninghaus (1828), the name *Craniolites brattenburgicus* was discarded in favour of Nilsson's *Crania tuberculata*. Lundgren (1885) suggested that *brattenburgicus* was a misspelling of *brattensburgensis* Retzius, a synonym of *C. craniolaris*. For more than 130 years *C. tuberculata* was in general use both as a species name and as the namebearer for the *Crania tuberculata* Zone (e.g. Różkowska 1955; Kongiel 1958).

In 1958 Carlsson, following a brief mention by Wind (1953), exhumed the name *C. brattenburgicus*, and his usage was followed by Kruytzer & Meijer (1958). In 1964 Rosenkrantz argued that Schlotheim's name should be discarded and that *C. tuberculata*, which he designated as the type species of a new subgenus (now a full genus) *Danocrania*, should replace it. We follow Rosenkrantz (1964) and Kruytzer (1969) in urging that Schlotheim's name should be discarded because he provided no species description and only a poor illustration, the species name was very similar to *C. brattensburgensis* Retzius (= *C. craniolaris* Linnaeus), the name had been out of general use for over a century, and its synonym *C. tuberculata* Nilsson is well understood and has been widely used as an informal zone name. An application for the suppression of Schlotheim's species name has been lodged with the ICZN.

In 1826 Nilsson described and figured four 'new' species of *Crania*, all of which, save *C. tuberculata*, were synonyms of previously described species. The following year he added to this list further species including *C. spinulosa* which he separated off from a redefined *C. tuberculata*.



Figs 26–28 *Danocrania tuberculata* (Nilsson). Specimens of Danian age from Faxe, Denmark. Fig. 26, interior of incomplete dorsal valve. BD3367, × 3. Figs 27–28, spinose ventral valve exterior and tuberculate valve interior. BD3366, × 3. See also Figs 23–25.

Figs 29–31 *Danocrania spinulosa* (Nilsson). Both specimens of Maastrichtian age from Inkerman, Crimea, U.S.S.R. Figs 29–30, exterior and interior of incomplete dorsal valve. BD3369, × 3. Fig. 31, ventral valve interior. BD3368, × 3.

In 1964, Rosenkrantz placed most spinose *Crania* in *Danocrania*, including all records of *C. spinulosa* save the original of Nilsson (1827). Since Nilsson's specimens are unavailable, and his figures closely resemble other *Danocrania* species, we have included *C. spinulosa* in this genus.

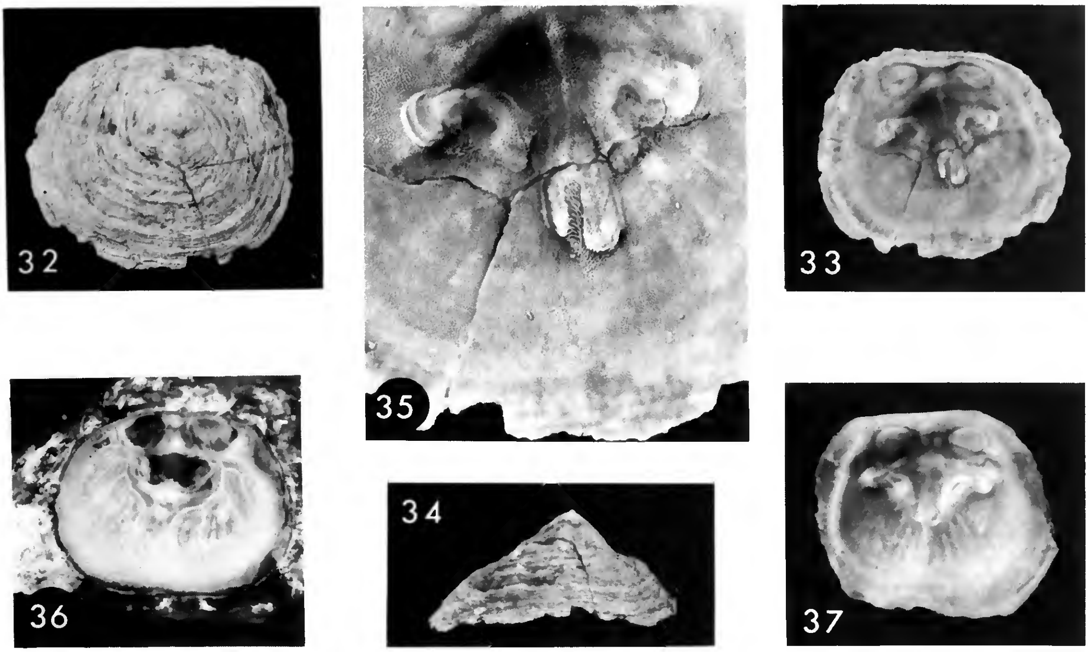
The new generic name *Westalicrania*, proposed by Cockbain (1967) for specimens closely resembling *Danocrania*, is here included in this genus.

Genus *NEOCRANIA* nov.

DIAGNOSIS. Ventral valve entirely cemented to substrate, often uncalcified, dorsal valve margins not thickened, with slightly raised muscle scars.

TYPE SPECIES. *Patella anomala* Müller (1776: 237; 1788: 4, pl. 5). Müller's original specimens are lost, but the species as it occurs in the North Atlantic is well known and undisputed. The title of Müller's monograph indicates that it occurs in the seas around Denmark or Norway, although he did not specify a locality for the species. We therefore do not select a neotype, in accordance with the recommendations of the ICZN (1985: 157–159; Article 75), but instead figure a specimen from off the Danish coast near where Müller's specimens may have been collected (Figs 32–36). Recent.

GENERIC NAME. There are extensive and confusing synonymies for the genus *Crania* (see for instance Dall 1871 and Williams *et al.* 1965). Two of the oldest available generic names are *Criopus* and *Criopoderma* of Poli 1791 and 1795 respectively. Following much of the contemporary practice of his day Poli used these two names for the soft parts and hard parts (the valves) of several brachiopods, with the result that inarticulates and articulates were united by him within these 'genera'. In modern taxonomy this is clearly unacceptable, and since the names



Figs 32–37 *Neocrania anomala* (Müller). Figs 32–36 are from 'Knähaken', south of Helsingborg, Øresund, Denmark, collected by the Elsinore Marine Laboratory, ZB3955a, b. Fig. 32, smooth dorsal valve exterior ornamented only by concentric growth-lines. × 2. Fig. 34, conical dorsal valve seen in lateral view. × 2. Figs 33, 35, dorsal valve interior showing details of anterior adductor muscle scars, and asymmetrical brachial protractor scar. × 2, × 5. Fig. 36, interior view of ventral valve with tissue still present, including posterior muscle fibres and mantle including gonadal ducts. × 2. Fig. 37, dorsal valve interior showing impressions of mantle canals. Cuming Collection, from the block figured by Reeve (1862: pl. 1, fig. 4). ZB134/23, × 2. North Atlantic. See also Figs 48–49.

have not been used (indeed Dall, 1871, did not accept them) other than as synonyms we are applying to the ICZN for their suppression.

Another old generic name, about which there has been considerable confusion, is *Orbicula* Cuvier 1798. The first description was very general in nature, but he mentioned *Patella anomala* Müller within the genus, so it became the type species. Illustrations were not provided until the third edition of Cuvier's *Règne Animal* (1845), at which time other species were added to *Orbicula* and the named species *O. lamellosa* (Broderip) was figured. That species is now the type of *Discinisca* Dall 1871, a chitinophosphatic-shelled impunctate discinid. *P. anomala* is a calcareous-shelled endopunctate craniid. Confusion as to whether *Orbicula* was a craniid or a discinid heightened when specimens sent by J. Sowerby to Lamarck were described (1819) as *Discina ostreoides*, and other examples from the same collection were described by G. B. Sowerby (in 1818, but not published until 1822) as *Orbicula norvegica*; all these specimens are discinids. Since then almost all nineteenth century authors treated *Orbicula* as a discinid; Sherborne (1932) listed 68 species names of *Orbicula* published between 1800 and 1850, of which only four should be craniids. From 1902 the *Zoological Record* notes only one non-synonymy use of the name *Orbicula*, which has thus essentially been unused taxonomically for over a century. Eminent specialists such as Davidson (1853) and Dall (1871) have recommended against the use of *Orbicula*, while recognizing that its original link with *P. anomala* placed it as a junior synonym of *Crania*. Davidson (1853) went on to recommend the suppression of *Orbicula*.

Thus in wishing to create a new genus based on *P. anomala* Müller, we are faced either with the need to reintroduce one of the above old named 'genera', a procedure which would create much confusion among zoologists and palaeontologists, or suppress these old names and start with a clean sheet using *Neocrania* gen. nov. We choose the latter course, and in addition to our application for the suppression of *Criopus* and *Criopoderma* we have applied to the ICZN for the suppression also of *Orbicula* Cuvier and for its inclusion on the Official Index of Rejected and Invalid Generic Names in Zoology.

INCLUDED SPECIES. **Patella anomala* Müller 1776. Figs 32–37, 48–49.
**Anomia turbinata* Poli 1795
Crania rostrata Hoeninghaus 1828
C. pourtalesi Dall 1871
C. nysti Davidson 1874
C. lecointei Joubin 1901
**C. huttoni* Thomson 1916
C. philippinensis Dall 1920
C. hawaiiensis Dall 1920
C. californica Berry 1921
**C. chathamensis* Allan 1940
C. valdiviae Helmcke 1940
C. roseoradiata Jackson 1952
C. indonesiensis Zezina 1981
**Neocrania reevei* nom. nov., pro *Crania suessii* Reeve 1862, non Bosquet 1859.

GEOGRAPHICAL RANGE. Cosmopolitan.

STRATIGRAPHICAL RANGE. Eocene–Recent.

DESCRIPTION. Shell of medium size (maximum length recorded 24 mm), subcircular to quadrangular in outline.

Ventral valve cemented to substrate by entire surface; valve varying from thin, uncalcified organic film to wholly calcified and thickened with anterolateral marginal rim. Valve interior with sometimes sunken posterior muscle scars with anterior scars united medially.

Dorsal valve smooth, slightly pustulose or finely ribbed, umbo centrally to posteriorly placed. Valve interior with large, widely separated pad-like posterior muscle scars and smaller diverging V-shaped anterior scars. Weak posterior submarginal rim, internal surfaces strongly endopunctate.

REMARKS. Although numerous names were applied to 'species' of living *Crania* between 1776 and 1862, most can be regarded as variants of *Neocrania anomala* (Müller) (Brunton & Curry 1979) or *N. turbinata* (Poli) (Logan 1979). Reeve (1862), in an important survey of living craniids, discussed the then known species and their distribution, and described a new species from Australia as *C. suessii*, a name which was unfortunately preoccupied by *C. suessi* of Bosquet (1859). We here propose the new name *Neocrania reevei* for the specimens from the Cuming collection (ZB 1520–1522) in the British Museum (Natural History) figured by Reeve (1862: pl. 1, fig. 2) and select ZB 1520 as the **lectotype**.

After the work of Dall (1871) no further comparisons between living and fossil craniid species of Cretaceous age were carried out until the present work, which follows a study of Recent and Tertiary *Neocrania* from New Zealand (Lee, in press).

Stratigraphical and geographical distribution

Although Rowell *in* Williams *et al.* (1965) gave a doubtful Carboniferous age for the oldest record of *Crania*, Williams & Wright (1970), following Rosenkrantz (1964), considered that '*Crania* s.s. is not reliably recorded in rocks older than the Cretaceous'. With the establishment

of the new genus *Neocrania* for Tertiary to Recent species formerly included in *Crania*, the stratigraphic range of *Crania* s.s. is reduced to the Upper Cretaceous (Senonian to Maastrichtian) in northwestern Europe and possibly the U.S.S.R. (Sobetskiĭ *et al.* 1982).

The oldest verified records of *Ancistrocrania*, *Isocrania* and *Danocrania* are also of Upper Cretaceous age, although Williams & Wright (1970) mentioned that '*Isocrania* . . . , like *Ancistrocrania* and *Craniscus*, is known from the Jurassic'. *Ancistrocrania* as presently defined may not extend into the Tertiary (Kruytzer 1969), but *Isocrania* and *Danocrania* continue up into the Danian and ?Thanetian respectively (Rosenkrantz 1964). It is worth noting that while the genera continue across the Cretaceous–Tertiary boundary, individual species disappear at the close of the Cretaceous (Surlyk & Johansen 1984). *Isocrania* is found as far afield as Africa and Asia, and *Danocrania* as Australia, though both are best known from the Chalk of Europe.

Ancistrocrania is recorded principally from Europe with one North American species. *Craniscus* ranges from the Jurassic through to the Recent, and appears to have had a wide distribution, although species records are poorly documented. As mentioned elsewhere in this paper, the differences between *Ancistrocrania* and *Craniscus* are small, and the somewhat puzzling dearth of Late Cretaceous records of *Craniscus* may be explained if some of the numerous species now assigned to *Ancistrocrania* should more correctly be placed in the former genus.

Neocrania appears to have had a cosmopolitan distribution from the Eocene to the present day.

Shell structure and form of growth

The shell structure of craniids has excited interest for well over a century and was studied by, for example, Carpenter (*in* Davidson 1853) and Blochmann (1892) and more recently, in great detail using the electron microscope, by Williams & Wright (1970). The early interest was aroused by the unusual endopunctation in living species, in which the distal ends of the puncta are branched. Williams & Wright (1970) illustrated the shell microstructure of *Neocrania anomala*, which they used to characterize the genus *Crania*; Mesozoic species of *Crania* s.s. were not knowingly studied. They also illustrated examples of *Isocrania egnabergensis* from Ignaberga; *Ancistrocrania parisiensis* from Ciply, Belgium; and '*Danocrania*' sp. from Ciply (we do not recognize the genus at this locality, and the specimen involved is, we believe, a *Crania antiqua*). These authors also discussed *Craniscus*, based on the living *C. japonicus* (Adams), as well as representative species from older Palaeozoic genera. Thus in terms of this paper Williams & Wright (1970) studied *Neocrania anomala*, *Isocrania egnabergensis*, *Crania antiqua*,

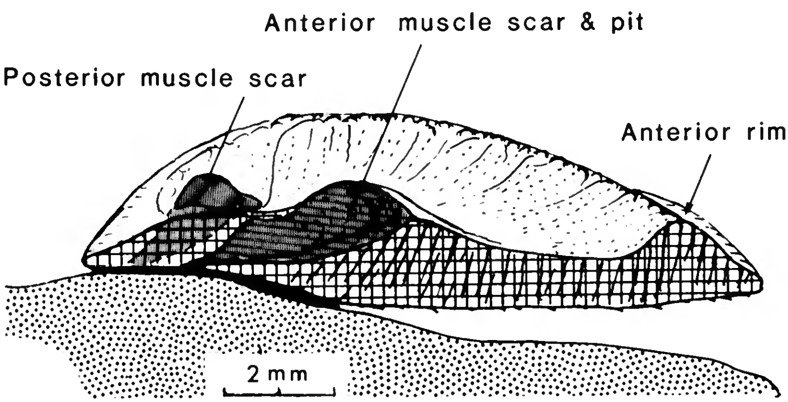


Fig. 38 *Crania craniolaris* (Linnaeus). Diagram of a ventral valve seen in median sagittal section, showing the anterior growth of the muscle scars, leaving pits behind them within the shell. (The posterior scars are not crossed by the median section.) An impression of the endopuncta is given on the sectioned and internal surfaces of the valve. See also Fig. 2.

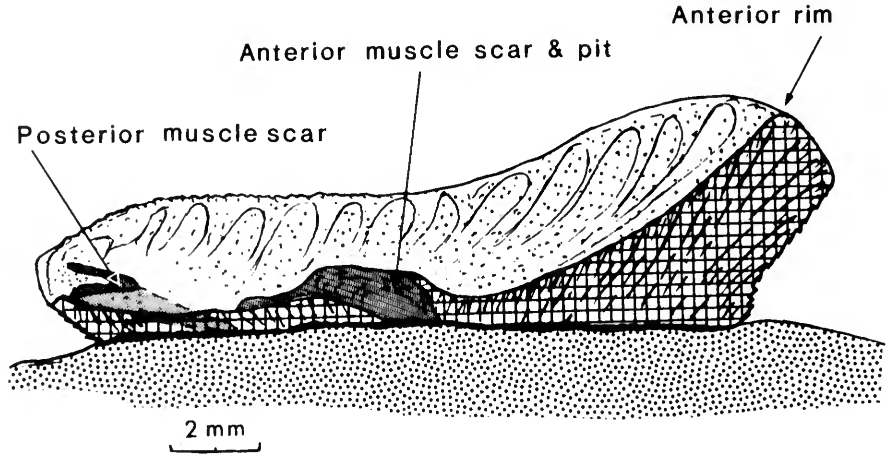


Fig. 39 *Ancistrocrania parisiensis* (Defrance). Diagram of a ventral valve seen in median sagittal section, showing the posterior growth of the muscle scars, leaving pits within the shell. An impression of the endopuncta is given on the sectioned and internal surfaces of the valve. See also Fig. 8.

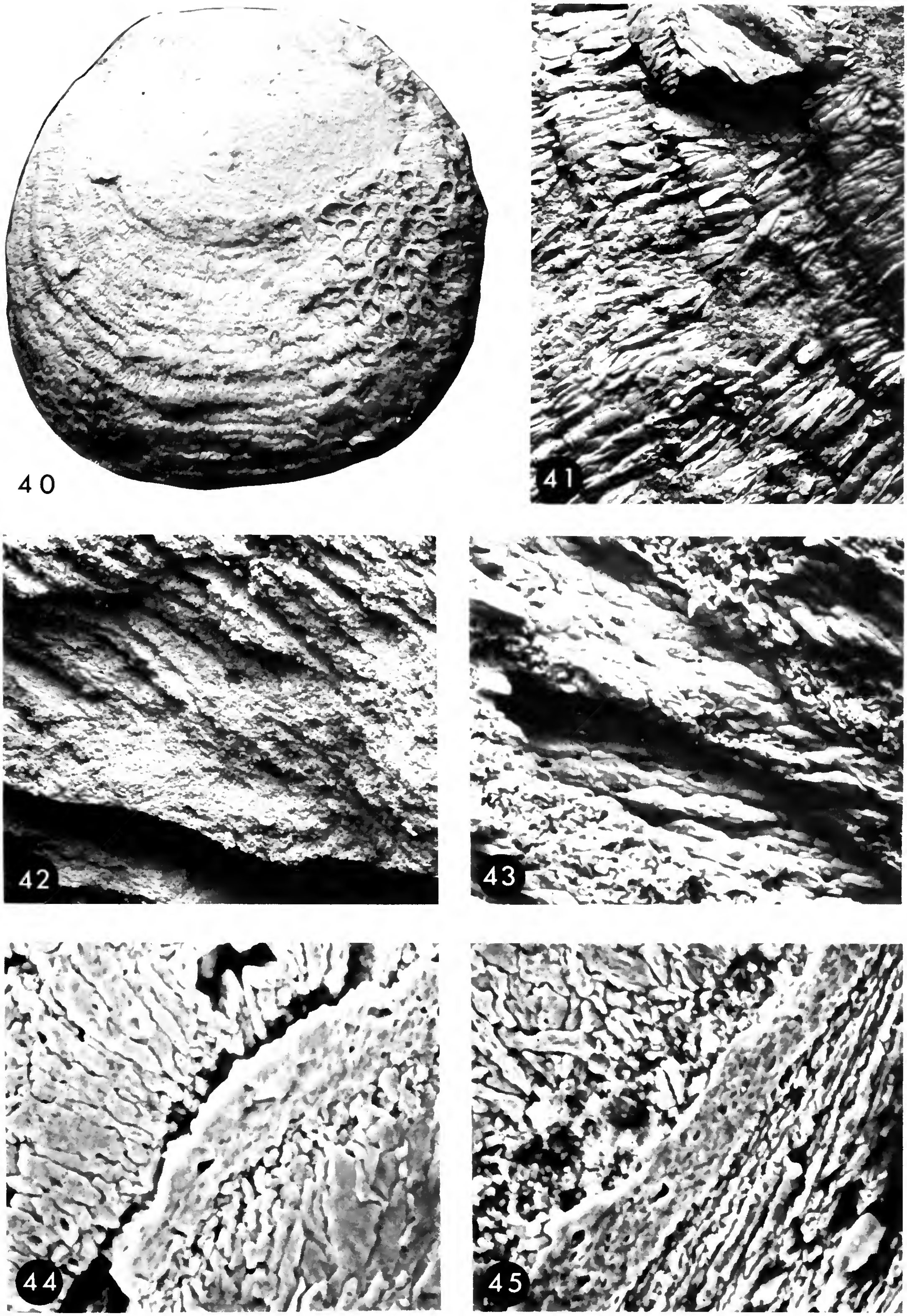
Ancistrocrania parisiensis and *Craniscus japonicus*, which we retain in that genus with some hesitation in view of the uncertainty surrounding the characteristics of *Craniscus tripartitus*—the type species—and its relationship with *Ancistrocrania*.

Using scanning electron microscopy we have studied examples of *N. anomala* from the Oban area of western Scotland; *C. craniolaris* from the type area of southern Sweden; *C. antiqua* from Ciply, Belgium; *A. parisiensis* from Ciply; and *D. tuberculata* from Faxe, Denmark. In general the attached ventral valves display more shell variation than dorsal valves, as noted by Williams & Wright (1970). This variation is principally linked with the degree of shell thickening in the ventral valve and involves the development of what the above authors termed 'canals'. These are tubular cavities (approximately 0·05 mm in diameter) with apertures up to twice that width on some interiors, and thus are several times wider than normal endopuncta. They are aligned obliquely to most external surfaces and extend inwards, roughly radially and anteriorly, so that their inner ends are more or less perpendicular to growth or internal surfaces. Such 'canals' are present in *Ancistrocrania parisiensis*, *A. davidsoni* (Davidson) and *Crania antiqua*;

Figs 40 to 45 are scanning electron micrographs taken in the Electron Microscope Unit of the British Museum (Natural History). Figs 40 and 41 are of uncoated specimens, taken using the environmental chamber, while the remainder are of specimens coated with gold-palladium.

Figs 40, 41 *Crania craniolaris* (Linnaeus). External views of the paralectotype 183B, of early Campanian age, Linnean Society Collection. Fig. 40, exterior of the complete ventral valve showing the posterior attachment scar (cicatrix) with concentric growth-lines anteriorly. × 8. Fig. 41, immediately anterolateral to the cicatrix (top right corner) showing secondarily enlarged crystals of the secondary layer. × 66. See also Figs 1–6.

Figs 42–45 *Crania antiqua* (Defrance). Ventral valves from Ciply, Belgium, of Maastrichtian age. Fig. 42, radial fracture surface of specimen B35519 showing inclined endopuncta. The exterior is to the top and the anterior to the right. × 85. Fig. 43, enlargement of an area with inclined endopuncta in the thickened shell anterior to the previous figure. × 600. Figs 44, 45. Two views of a mid-radial section (resin-mounted, polished and etched) showing what Williams & Wright (1970: pl. 11, fig. 2) called the 'micritic rubble junction between the secondary laminae . . . and the separation layer . . .'. Specimen B82746, × 1100. Fig. 44, near the cicatrix (bottom right), below the region of the posterior muscle scars, showing secondary laminae, the junction layer and the coarse fabric between the endopuncta. Fig. 45, similar coarse fabric near the posterior margin, beyond the cicatrix, showing the junction layer. Valve exterior is to the bottom right.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see below for further discussion on these structures. We have not seen normally-sized endopuncta with these 'canals', nor have we distinguished external branching in these genera, such as occurs in the endopuncta of *Neocrania*.

In our view *Crania* s.s. and *Ancistrocrania* differ principally on their modes of growth away from their areas of initial attachment. Adult *Crania* species have posterior attachment scars and thus normally grew mainly anteriorly during life. Since the main muscles were inserted onto the ventral valve from its earliest stages, in valves which are heavily thickened they leave a trace or cavity from their adult internal surface positions back to their youthful positions within the attachment scar. Thus in *Crania* s.s. the anterior (and to a lesser extent also the posterior) scars trace into the shell posteriorly (Fig. 38).

In thick-shelled species of *Ancistrocrania* the adult attachment is positioned anterocentrally (*A. davidsoni*), or involves almost the complete external surface (*A. parisiensis*). Growth-lines show the initial attachment to have been anterocentral in all species, and thus growth was virtually holoperipheral, with a strong posterior component. The traces or cavities of the muscle scars within the shell, therefore, have their origins anterocentrally, and this resulted in anteriorly-directed muscle cavities (Fig. 39).

This marked difference in the extent of attachment areas in *A. parisiensis* and *A. davidsoni* is the only obvious difference between the species, and the possibility that it may have resulted by chance settlement of the spat onto large hard surfaces or onto small hard objects, respectively, must be recognized.

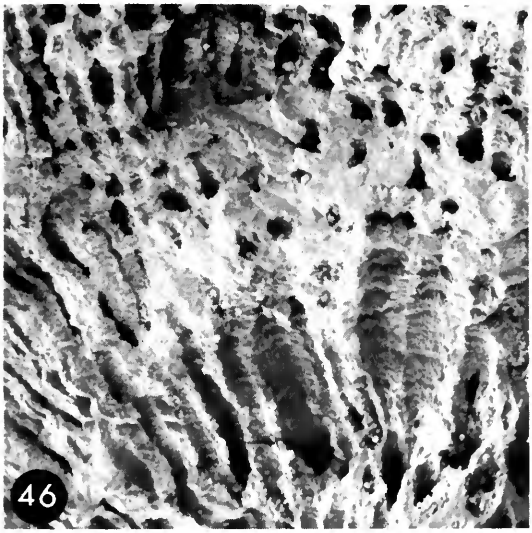
In general the degree of cemented attachment to the substrate of craniid ventral valves is variable, but consistent within species. All known species attach to the substrate at least initially, but those individuals surviving to adulthood vary as to the substrate type and degree of cementation. Surlyk (1973) showed how *Isocrania egnabergensis* and *I. costata*, although living on different substrates, became unattached during ontogeny and lived freely on, or slightly below, the sediment. It seems that some *Danocrania* species retained a small posterior attachment, while others may have become free-living as adults. The two species of *Crania* s.s. included here both attached by up to a third of their adult ventral valve area, while living *Neocrania* species attach the whole of their ventral valves to the substrate, as also seems to be the situation in *Craniscus*.

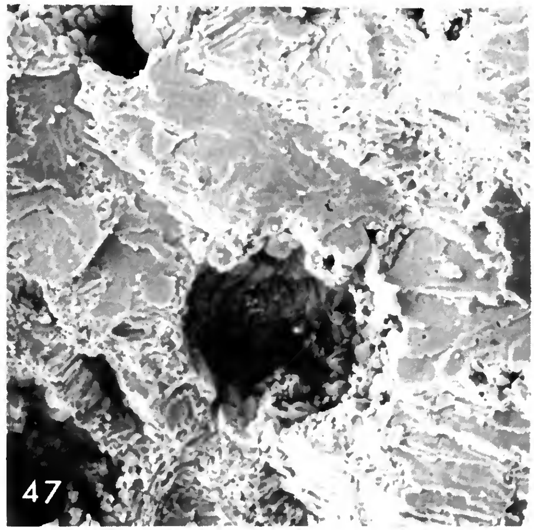
Endopuncta and 'canals'

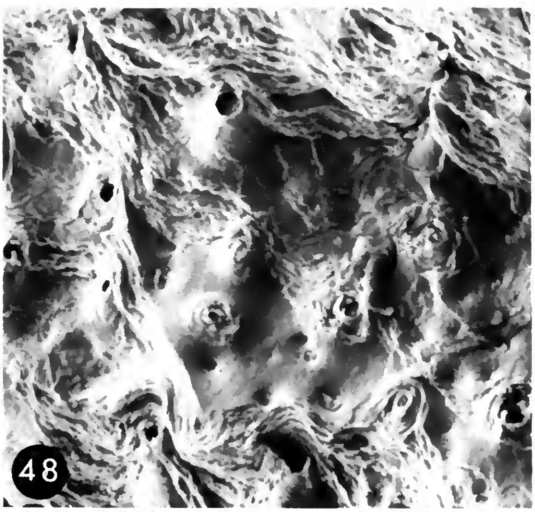
We believe the 'canals' recorded by Williams & Wright (1970) to be enlarged endopuncta, developed in the thickened ventral valves of some *Crania* and *Ancistrocrania* species, which may have been developed as a means of limiting the amount of calcium carbonate required for these thick valves.

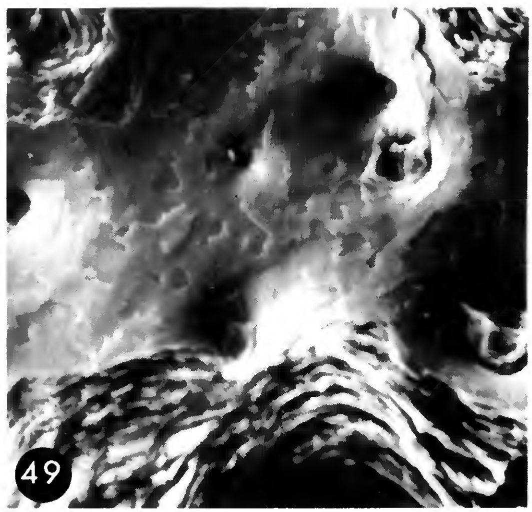
In *Ancistrocrania parisiensis* and *A. davidsoni* the diameter of the puncta increases with increased valve thickness, i.e. at the anterior rim and around the anterior muscle scars their diameters increase to the extent of allowing the elimination of up to 50% of the valve material (Figs 45, 46). The diameter of these puncta decreased considerably as the shell growth ceased, so that on mature internal surfaces they are much less obvious than on eroded, broken or younger specimens. Earlier we described the oblique nature of these wide puncta. This is especially clearly developed in an anterior direction and associated with highly thickened marginal rims. It resulted from the speed of growth and deposition of shell material in these thickened areas which, as it were, pulled the endopuncta in the principal direction of growth. As growth slowed, later in life, the puncta curved to the more usual orientation, approximately perpendicular to the inner surface. In thinner, median regions of the valve similar wide puncta remained perpendicular to both surfaces through growth, simply because less shell material was added to the valve, only increasing its thickness rather than also adding to its size.

As the thickness of ventral valves varies between species we do not find the absence or presence of wide puncta particularly helpful in defining genera. However, it is relevant that the puncta in species of *Danocrania*, *Isocrania* and *Neocrania* remain relatively narrow, seldom exceeding about 0·002 mm in diameter.









Figs 46 to 49 are scanning electron micrographs taken in the Electron Microscope Unit of the British Museum (Natural History). Specimens coated with gold-palladium.

Figs 46, 47 *Ancistrocrania davidsoni* (Davidson), from the Maastrichtian chalk of Ciply, Belgium. B3552. View showing a fractured mid-radial section of a ventral valve near the thickened anterior margin. Interior is to the top and anterior to the left. Fig. 46, at about the mid-thickness of the shell, showing the large, closely packed endopuncta. × 50. Fig. 47, enlargement from the middle of the previous figure showing the lamellose appearance of the fractured surface between the endopuncta. × 350. See also Figs 10–14.

Figs 48, 49 *Neocrania anomala* (Müller), from off the west coast of Scotland. Dorsal valve ZB3967, viewed on a fractured surface. The exterior is uppermost. Fig. 48, showing the outwardly deflected lamellae around endopuncta. × 290. Fig. 49, detail from the previous figure showing the pattern of screw dislocations on the laminae and small scale inwardly-directed cone-in-cone structures forming small tubercules on the internal surface. × 1100. See also Figs 32–37.

Shell fabric and relationships

Bearing in mind that Williams & Wright (1970) used living *Neocrania anomala* to characterize the shell of '*Crania*', all we can add to their description is that the ventral valves of some *Neocrania* species are thickened and display, at about × 200, a prismatic structure orientated with the endopunctation, which at over × 1000 can be seen to be composed of compact laminae similar to those figured in the dorsal valve of *Neocrania* (Figs 48–49).

The fabric of a ventral valve of *Crania antiqua* (Figs 44–45) was described by Williams & Wright (1970) as *Danocrania*, and their information, combined with our own observations on *Crania craniolaris* dorsal and ventral valves, shows an essentially laminar shell with endopuncta of varied size, including the so-called 'canals' in *C. antiqua*. The studied ventral valve of *Danocrania* has a uniformly endopunctate laminar shell, apparently lacking the 'crystalline' fabric of Williams & Wright (1970).

We have been unable to find Mesozoic *Craniscus* specimens with shell well preserved, and can add nothing further to the earlier studies using *C. japonicus*. We agree, however, with Williams & Wright (1970) that the dorsal valve morphology of *Craniscus* is close to that of *Ancistrocrania*. *Isocrania* species are distinctive, but are probably more closely related to *Danocrania* than to other genera. *Danocrania*, *Crania* and *Neocrania* form a grouping with species of the last two genera forming an evolutionary lineage.

Acknowledgements

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Lectotype selections for Ordovician trilobites from the Girvan District, Strathclyde

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Synopsis

Thirty-two lectotypes are selected for species of trilobites of Upper Ordovician age described by Etheridge & Nicholson (1878–80) and by Reed (1903–44) from the Girvan District, Strathclyde. A further five lectotypes are selected for species placed in synonymy.

Introduction

In the course of preparing the *Catalogue of the Type and Figured Specimens of Trilobita in the British Museum (Natural History)* (Morris & Fortey 1985), and a computer catalogue of the Gray Collections (Tripp & Howells 1981), the need to select lectotypes wherever possible has become apparent. The Gray Collection was purchased by the Trustees in 1920 and was received at the Museum in that year; specimens subsequently collected by Mrs Robert Gray and her daughters were presented to the Museum from time to time. T. H. Withers registered the figured, mentioned and named specimens between 1920 and 1924. Most of the remainder of the collection was determined by Tripp and registered by R. Baker between 1947 and 1949. Apart from figured or mentioned specimens, it is uncertain how many specimens were studied by Nicholson & Etheridge or by Reed. In some cases the syntypes are not all conspecific; in many the original drawings are not adequate for comparison. In this paper lectotypes are selected and figured for 32 species considered to be taxonomically valid. In addition, lectotypes are selected for five species placed in synonymy. Species belonging to the family Odontopleuridae are under revision by J. K. Ingham, and are not discussed herein.

The definitive account of the stratigraphy and faunas of the Girvan District is that of Charles Lapworth (1882); this was followed up by the Geological Survey Memoir of Peach & Horne (1899). Both these works made extensive use of Mrs Gray's Collection, and of Nicholson & Etheridge's Monograph based on her collection. More recently the Barr (Llandeilo) and Lower Ardmillan (Caradoc) Series were revised by Williams (1962), and the Drummuck Group (Upper Ashgill) by Harper (1982). The Whitehouse Group (Lower Ashgill) is under revision by Ingham.

Deposition of Material

The majority of the specimens considered are in the British Museum (Natural History) (BM). Other institutions housing Girvan material are: Hunterian Museum, Glasgow (HM A); British Geological Survey, Edinburgh (BGSE); and Oxford University Museum (OUM).

Systematics

Family **REMOPLEURIDIDAE** Hawle & Corda, 1847

Genus ***REMOPLEURIDES*** Portlock, 1843

TYPE SPECIES. By subsequent designation of Miller (1889: 566); *Remopleurides colbii* Portlock (1843: 256), from the Killey Bridge Formation (Ashgill) of Pomeroy district, Co. Tyrone, Northern Ireland.

Remopleurides asteroideus Reed, 1935
(Pl. 1, fig. 7)

1935 *Remopleurides asteroideus* Reed: 11; pl. 4, figs 6, 7.

LECTOTYPE. Selected herein: HM A 933 (= BG 2066), from the Starfish Bed, South Threave Formation, of South Threave, near Girvan, Strathclyde. Grid Ref. NS 250038.

Remopleurides craigensis Reed, 1935
(Pl. 2, figs 9–11)

1903 *Remopleurides* cf. *nanus* Leuchtenberg; Reed: 41; pl. 6, figs 16, 17.
1935 *Remopleurides craigensis* Reed: 10; pl. 1, figs 18, 18a.

LECTOTYPE. Selected herein: BGSE 5100 (= JS 5101), original of Reed, 1935: pl. 1, figs 18, 18a, from the Craighead Limestone, Upper Ardwell Group (Caradoc) of Craighead, near Girvan, Strathclyde. Grid Ref. NX 234013.

Remopleurides nicholsoni Reed, 1914
(Pl. 1, fig. 8)

1879 *Remopleurides colbii*? Portlock; Nicholson & Etheridge: 146; pl. 10, figs 8, 8a.
1903 *Remopleurides colbii* Portlock; Reed: 36; pl. 5, figs 17, 17a, b.
1914 *Remopleurides nicholsoni* Reed: 12; pl. 2, figs 3–9.

LECTOTYPE. Selected herein: BM In.21038, original of Reed, 1903: pl. 5, figs 17, 17a, b, from the Ladyburn Formation, Upper Drummuck Group (Rawtheyan) of Drummuck, near Girvan, Strathclyde. Grid Ref. NS 235032.

Genus ***TERATORHYNCHUS*** Reed, 1903

TYPE SPECIES. By monotypy; *Remopleurides* (*Teratorhynchus*) *bicornis* Reed, 1903, from the Caradoc of Girvan, Strathclyde.

Teratorhynchus bicornis (Reed, 1903)
(Pl. 1, figs 1, 4)

1903 *Remopleurides* (*Teratorhynchus*) *bicornis* Reed: 33; pl. 5, figs 5–16.
1914 *Telephus salteri* Reed: 16; pl. 2, fig. 11.
1980 *Teratorhynchus bicornis* (Reed); Tripp: 132; pl. 1, fig. 31.

LECTOTYPE. Selected herein: BM In.21009, original of Reed, 1903: pl. 5, figs 5, 6, from the Lower Balclatchie Group (Caradoc) of Dow Hill, near Girvan, Strathclyde. Grid Ref. NX 190960. The holotype, by monotypy, of *Telephus salteri* Reed is BM In.21179, from the Upper Balclatchie Group of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Family **ASAPHIDAE** Burmeister, 1843

Genus ***ISOTELUS*** DeKay, 1824

TYPE SPECIES. By subsequent designation of Bassler, 1915; *Isotelus gigas* DeKay, 1824, from middle Ordovician of New York State, U.S.A.

Isotelus girvanensis (Reed, 1931)
(Pl. 1, fig. 3)

1903 *Asaphus* (*Isotelus*) *gigas* DeKay; Reed: 45; pl. 7, fig. 1.
1931 *Asaphus* (*Isotelus*) *girvanensis* Reed: 10.
1980 *Isotelus girvanensis* (Reed); Tripp: 132.

LECTOTYPE. Selected herein: BM In.21560, original of Reed, 1903: pl. 7, fig. 1, from the Lower Ardwell Group (Caradoc) of Ardmillan, near Girvan, Strathclyde. Grid Ref. NX 168940.

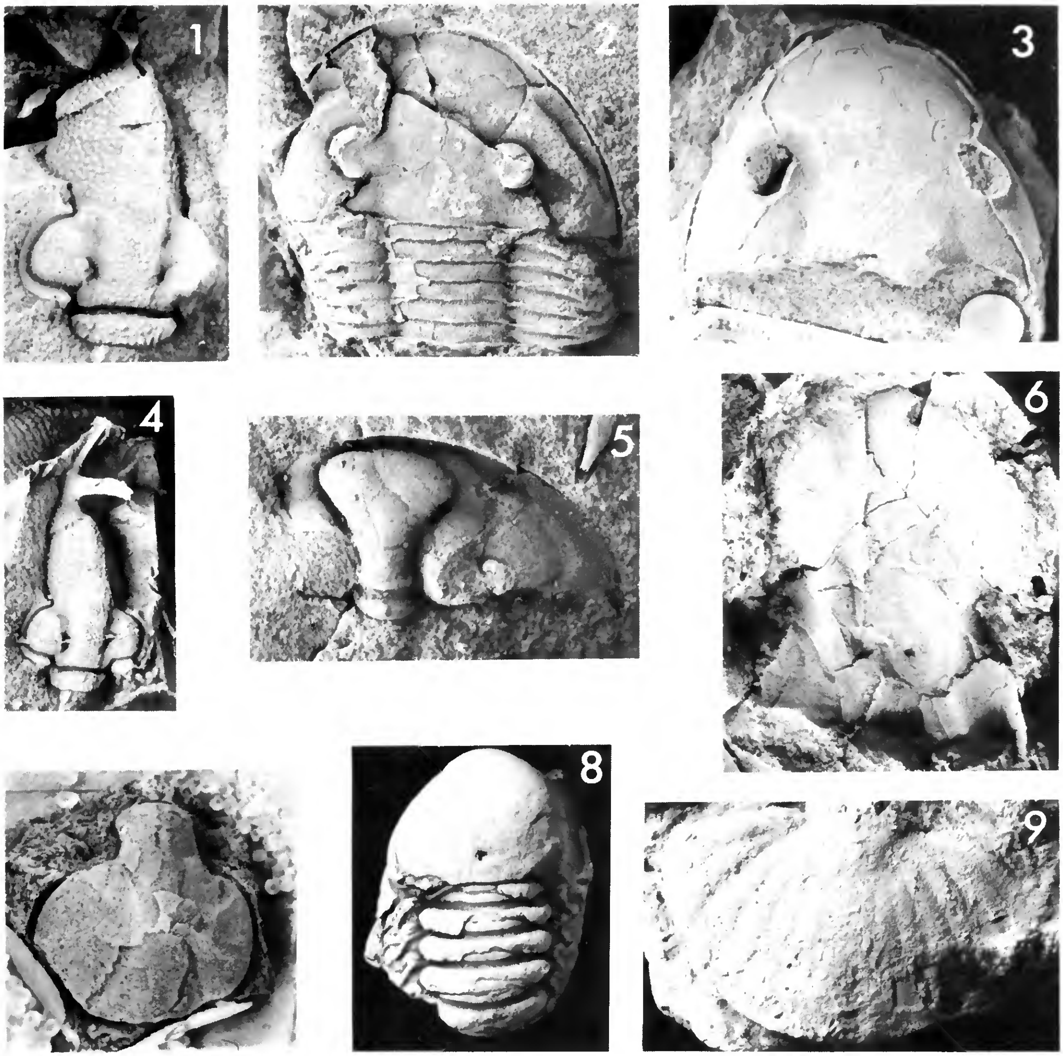


PLATE 1

Figs 1, 4 *Teratorhynchus bicornis* (Reed, 1903), Lower Balclatchie Group, Dow Hill. Cranidium, figd Reed, 1903: pl. 5, figs 5, 6. BM In.21009. Fig. 1, × 3; Fig. 4, latex cast from external mould, × 1·75.

Fig. 2 *Isotelus instabilis* (Reed, 1903), Lower Balclatchie Group, Dow Hill. Cephalon and 6 thoracic segments, figd Reed, 1904: pl. 7, fig. 6. BM In.21584. × 3.

Fig. 3 *Isotelus girvanensis* (Reed, 1931), Lower Ardwell Group, Ardmillan. Cephalon, figd Reed, 1904: pl. 7, fig. 1. BM In.21560, × 2·2.

Fig. 5 *Raymondaspis ardmillanensis* (Reed, 1904), Lower Ardwell Group, Ardmillan. Cephalon, figd Reed, 1904: pl. 13, figs 1, 1a. BM In.22675. × 3.

Fig. 6 *Isotelus grayae* (Reed, 1914), Upper Balclatchie Group, Balclatchie. Cranidium, figd Reed, 1914: pl. 3, fig. 2. BM In.21567. × 2·2.

Fig. 7 *Remopleurides asteroideus* (Reed, 1935), South Threave Formation, Starfish Bed. Cranidium, figd Reed, 1935: pl. 4, fig. 6. HM A 933. × 4.

Fig. 8 *Remopleurides nicholsoni* Reed, 1914, Ladyburn Formation, Drummuck. Cephalon and 4 thoracic segments, figd Reed, 1903: pl. 5, figs 17, 17a, 17b. BM In.21038. × 1·75.

Fig. 9 *Eobronteus craigensis* (Reed, 1904). Upper Ardwell Group, Craighead Quarry. Pygidium, figd Reed, 1904: pl. 12, fig. 12. BM In.22668. × 1·75.

Isotelus grayae (Reed, 1914)
(Pl. 1, fig. 6)

1914 *Asaphus* (*Isotelus*) *grayae* Reed: 16; pl. 3, figs 1–6.
1931 *Asaphus* (*Isoteloides*) *grayae* Reed; Reed: 10.
1980 *Isotelus grayae* (Reed); Tripp: 132.

LECTOTYPE. Selected herein: BM In.21567, original of Reed, 1914: pl. 3, fig. 2, from the Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Isotelus instabilis (Reed, 1903)
(Pl. 1, fig. 2)

1903 *Asaphus* (*Isotelus*) *instabilis* Reed: 46.
1904 *Asaphus* (*Isotelus*) *instabilis* Reed; Reed: pl. 7, figs 2–8.
1980 *Isotelus instabilis* (Reed); Tripp: 132.

LECTOTYPE. Selected herein: BM In.21584, original of Reed, 1904: pl. 7, fig. 6, from the Lower Balclatchie Group (Caradoc) of Dow Hill, near Girvan, Strathclyde. Grid Ref. NX 192961.

Family **STYGINIDAE** Vogdes, 1890

Genus ***RAYMONDASPIS*** Přibyl, 1949

TYPE SPECIES. By subsequent designation of Miller (1889: 550); *Holometopus limbatus* Angelin, 1854, from the *expansus* or *lepidurus* Zone (late Arenig–early Llanvirn) of Fågelsång, Scania, Sweden.

Raymondaspis ardmillanensis (Reed, 1904)
(Pl. 1, fig. 5)

1904 *Bronteopsis ardmillanensis* Reed: 92; pl. 13, figs 1–4.
1914 *Bronteopsis ardmillanensis* Reed; Reed: 26; pl. 4, fig. 7.
1980 *Raymondaspis ardmillanensis* (Reed) Tripp: 132.

LECTOTYPE. Selected herein: BM In.22675, original of Reed, 1904: pl. 13, figs 1, 1a, from the Lower Ardwell Group (Caradoc) of Ardmillan, near Girvan, Strathclyde. Grid Ref. NX 168940.

Family **SCUTELLUIDAE** Richter & Richter, 1955

Genus ***EOBRONTEUS*** Reed, 1928

TYPE SPECIES. By original designation; *Entomostracites laticauda* Wahlenberg, 1818, from the Upper Leptaena Limestone (Ashgill) of Dalarna, Sweden.

Eobronteus craigensis (Reed, 1904)
(Pl. 1, fig. 9)

1904 *Bronteus craigensis* Reed: 89; pl. 12, figs 12, 13.
1928 *Bronteus* (*Eobronteus*) *craigensis* Reed; Reed: 51.
1980 *Eobronteus craigensis* (Reed); Tripp: 149.

LECTOTYPE. Selected herein: BM In.22668, original of Reed, 1904: pl. 12, fig. 12, from the Craighead Limestone (Caradoc) of Craighead Quarry, near Girvan, Strathclyde. Grid Ref. NX 234013.

Genus ***FAILLEANA*** Chatterton & Ludvigsen, 1976

TYPE SPECIES. By original designation; *Failleana calva* Chatterton & Ludvigsen, 1976, from middle Ordovician of Canada.

Failleana*? *memorabilis (Reed, 1906)
(Pl. 2, fig. 8)

1904 *Illaenus* cf. *oculosus* Holm; Reed: 71; pl. 10, fig. 11.
1906 *Illaenus memorabilis* Reed: 165; pl. 20, fig. 9.

LECTOTYPE. Selected herein: BM In.21814, original of Reed, 1906: pl. 20, fig. 9, from the Lower Balclatchie Group (Caradoc) of Dow Hill, near Girvan, Strathclyde. Grid Ref. NX 192961.

REMARKS. This cranidium is clearly that of an effaced scutelluid, as evinced by the long rhachial furrows and fossulae. In these features it resembles *Failleana* Chatterton & Ludvigsen, 1976, but the eyes are situated more posteriorly than in other members of that genus, and we attribute *memorabilis* to it with reserve.

Family ILLAENIDAE Hawle & Corda, 1847

Genus *ILLAENUS* Dalman, 1827

TYPE SPECIES. By subsequent designation of Pictet, 1854: 515; *Entomostracites crassicauda* Wahlenberg, 1818, from the Crassicauda Limestone (Llandeilo) of Fjäcka, Dalarna, Sweden.

Illaenus peachi Reed, 1914
(Pl. 2, fig. 2)

1914 *Illaenus peachi* Reed: 24; pl. 4, figs 2, 3, 3a.

LECTOTYPE. Selected herein: BM In.21909, original of Reed, 1914: pl. 4, figs 3, 3a, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Illaenus richardsoni Reed, 1914
(Pl. 2, fig. 5)

1914 *Illaenus richardsoni* Reed: 25; pl. 4, figs 4, 5, 5a.

LECTOTYPE. Selected herein: BM In.21913, original of Reed, 1914: pl. 4, figs 5, 5a, from the Lower Ardwell Group (Caradoc) of Ardmillan, near Girvan, Strathclyde. Grid Ref. NX 169938.

Genus *NANILLAENUS* Jaanusson, 1954

TYPE SPECIES. By original designation; *Illaenus conradi* Billings, 1859, from middle Ordovician, Black River Group of Ottawa, Canada.

Nanillaenus superstes (Reed, 1944)
(Pl. 2, fig. 7)

1904 *Illaenus* cf. *oculosus* Holm; Reed: 71; pl. 10, figs 9, 10.
1944 *Illaenus superstes* Reed: 59; pl. 2, figs 3–6.
1980 *Nanillaenus superstes* (Reed) Tripp: 132.

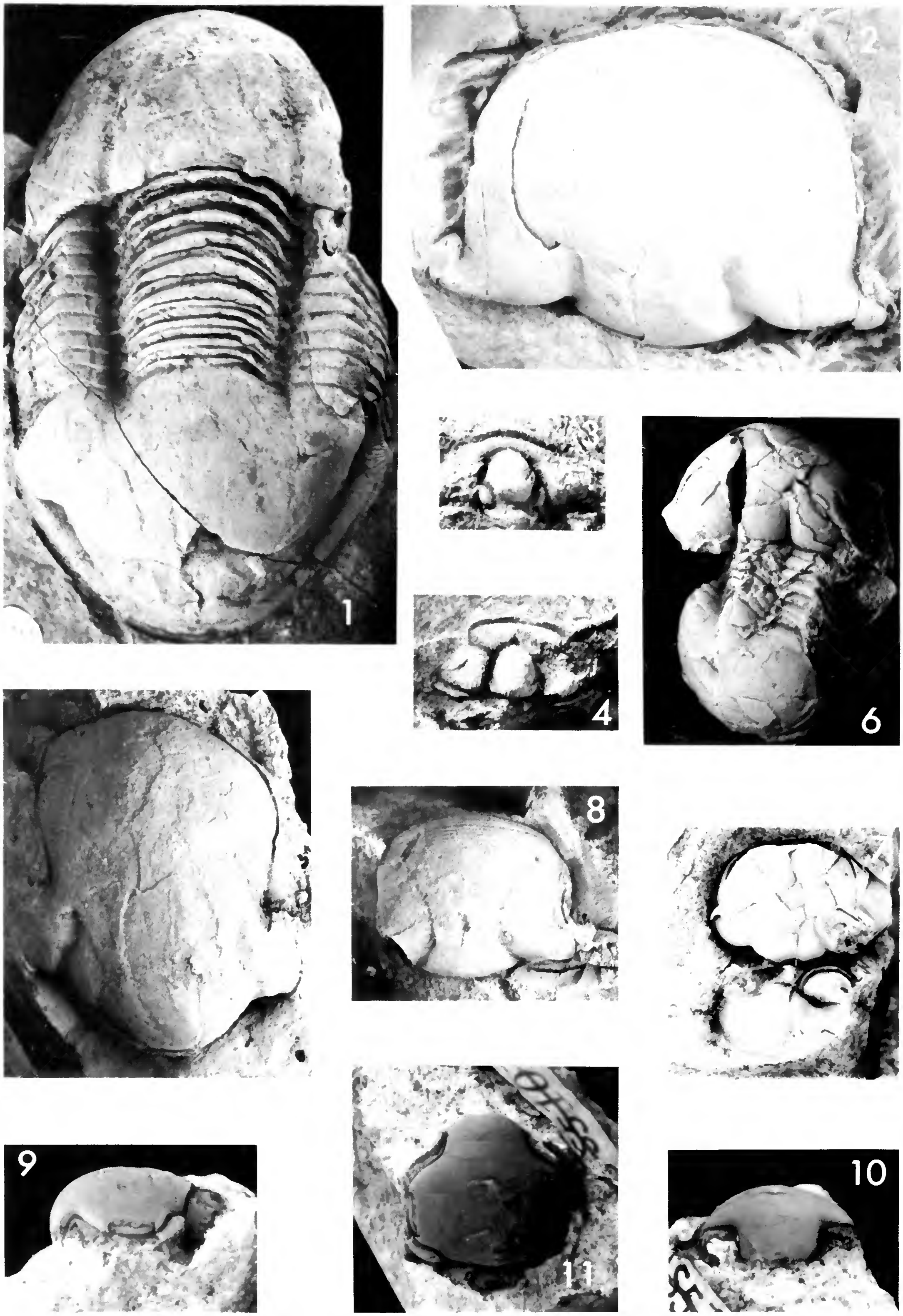
LECTOTYPE. Selected herein: HM A 3630, original of Reed, 1944: pl. 2, figs 3, 3a, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Genus *STENOPAREIA* Holm, 1886

TYPE SPECIES. By original designation; *Illaenus Linnarssonii* Holm, 1882, from the Boda Limestone (Ashgill) of Dalarna, Sweden.

Stenopareia balclatchiensis (Reed, 1904)
(Pl. 2, fig. 6)

1904 *Illaenus balclatchiensis* Reed: 56; pl. 8, figs 12–16.
1935 *Illaenus balclatchiensis cristata* Reed: 24; pl. 3, fig. 2.
1980 *Stenopareia balclatchiensis* (Reed) Tripp: 127; pl. 2, fig. 9.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LECTOTYPE. Selected Tripp (1980: 127), original of Reed, 1904: pl. 8, fig. 14, BM In.21730, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969. (In Tripp (1980) the register number of the lectotype was wrongly quoted as BM In.21727; it should have been as given above.) The holotype, by monotypy, of *cristata* Reed is HM A 935 (BG 25), from the Lower Balclatchie Group (Caradoc) of Dow Hill, near Girvan, Strathclyde. Grid Ref. NX 192961.

REMARKS. Tripp (1980: pl. 2, fig. 2) illustrated BM In.21722 both as the lectotype (= BM In.21730) and as BM In.21727.

Stenopareia nexilis (Salter, 1867)
(Pl. 2, fig. 1)

1867 *Illaenus* (*Dysplanus*) *nexilis* Salter: 190; pl. 30, figs 4, 5.
1935 *Illaenus fluvialis* Reed: 13; pl. 2, figs 1–3.
1935 *Illaenus longicapitatus subcarinata* Reed: 19; pl. 2, figs 8, 8a.
1944 *Illaenus drummuckensis* Reed *in* Reed & Begg: 260; pl. 1, figs 3, 4.
1982 *Stenopareia nexilis* (Salter) Howells: 13.

LECTOTYPE. Selected herein: OUM C2, original of Salter, 1867: pl. 30, fig. 4, from the Ladyburn Formation? (Rawtheyan) of Drummuck, near Girvan, Strathclyde. Grid Ref. NS 235032. The lectotype of *Illaenus fluvialis* Reed, selected herein, is BGSE 5101, original of Reed, 1935: pl. 2, fig. 1; the lectotype of *subcarinata* Reed, selected herein, is BGSE 5108, original of Reed, 1935: pl. 2, fig. 8. The holotype of *drummuckensis* Reed is HM A 3687 (= BG 6454). The last three taxa are all from the South Threave Formation (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038.

REMARKS. There is no evidence of the occurrence of more than one species of *Stenopareia* in the Upper Drummuck Group of the Girvan district.

Family **AULACOPLEURIDAE** Angelin, 1854

Genus ***OTARION*** Zenker, 1833

TYPE SPECIES. By monotypy; *Otarion diffractum* Zenker, 1833, from the Kopanina Beds (Ludlow) of Dlouhá hora, near Beroun, Czechoslovakia.

PLATE 2

Fig. 1 *Stenopareia nexilis* (Salter, 1867), Ladyburn Formation, Drummuck. Dorsal shield, figd Salter, 1867: pl. 30, fig. 5. OUM C.2. × 1·5.

Fig. 2 *Illaenus peachi* Reed, 1914, Upper Balclatchie Group, Balclatchie. Cranidium, figd Reed, 1914: pl. 4, figs 3, 3a. BM In.21909. Oblique anterior view, × 2.

Fig. 3 *Otarion* (s.l.) *tumidum* Reed, 1935, Upper Balclatchie Group, Balclatchie. Cranidium, figd Reed, 1935: pl. 1, fig. 21. BM In.36921. × 7.

Fig. 4 *Toernquistia translata* (Reed, 1931), Upper Balclatchie Group, Balclatchie. Cranidium, figd Reed, 1906: pl. 12, fig. 3. BM In.22641. × 5.

Fig. 5 *Illaenus richardsoni* Reed, 1914, Lower Ardwell Group, Ardmillan. Cranidium, figd Reed, 1914: pl. 4, figs 5, 5a. BM In.21913. Oblique anterior view, × 2·5.

Fig. 6 *Stenopareia balclatchiensis* (Reed, 1904), Upper Balclatchie Group, Balclatchie. Dorsal shield lacking free cheeks, figd Reed, 1904: pl. 8, fig. 14, BM In.21730. × 3.

Fig. 7 *Nanillaenus superstes* (Reed, 1944), Upper Balclatchie Group, Balclatchie. Disassociated dorsal shield, figd Reed, 1944: pl. 2, figs 3, 3a. HM A 3630. × 4.

Fig. 8 *Failleana*? *memorabilis* (Reed, 1906), Lower Balclatchie Group, Dow Hill. Cranidium, figd Reed, 1906: pl. 20, fig. 9. BM In.21814. × 2.

Figs 9–11 *Remopleurides craigensis* Reed, 1935, Upper Ardwell Group, Craighead. Cranidium, figd Reed, 1935: pl. 1, fig. 18. BGSE 5100. Left lateral, anterior and dorsal views, × 3.

Otarion (s.l.) ***tumidum*** Reed, 1935
(Pl. 2, fig. 3)

1935 *Otarion tumidus* Reed: 43; pl. 1, figs 21, 21a.

LECTOTYPE. Selected herein: BM In.36961, original of Reed, 1935: pl. 1, figs 21, 21a, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Subgenus ***AULACOPLEURA*** Hawle & Corda, 1847

TYPE SPECIES. By monotypy; *Arethusina Koninckii* Barrande, 1846: 48, from the Wenlock Series of Czechoslovakia.

Otarion (***Aulacopleura***) ***reedi*** (Přibyl, 1947)
(Pl. 3, fig. 2)

1904 *Arethusina konincki*? Barrande; Reed: 83; pl. 11, figs 14, 15.
1947 *Aulacopleura* (*Paraaulacopleura*) *reedi* Přibyl: 541.
1980 *Otarion* (*Aulacopleura*) *reedi* (Přibyl) Tripp: 132.

LECTOTYPE. Selected herein: BM In.21972, original of Reed, 1904: pl. 11, fig. 14, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Family **DIMEROPYGIDAE** Hupé, 1953

Genus ***TOERNQUISTIA*** Reed, 1896

TYPE SPECIES. By subsequent designation of Warburg, 1925: 198; *Cyphaspis* (*Törnquistia*) *Nicholsoni* Reed, 1896, from the Keisley Limestone (Ashgill) of Keisley Quarry, Cumbria. Grid Ref. NY 713238.

Toernquistia translata (Reed, 1931)
(Pl. 2, fig. 4)

1904 *Menocephalus*? (*Törnquistia*) cf. *nicholsoni* Reed: 86; pl. 12, figs 3–7.
1931 *Hystricurus translatus* Reed: 8.
1980 *Toernquistia translata* (Reed) Tripp: 132.

LECTOTYPE. Selected herein: BM In.22641, original of Reed, 1904: pl. 12, fig. 3, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Family **RAPHIOPHORIDAE** Angelin, 1854

Genus ***AMPYX*** Dalman, 1827

TYPE SPECIES. By monotypy; *Asaphus* (*Ampyx*) *nasutus* Dalman, 1827, from the Upper Arenig of Västanå, Sweden.

Ampyx hornei Etheridge & Nicholson, 1879
(Pl. 3, fig. 1)

1879 *Ampyx hornei* Etheridge & Nicholson: 184; pl. 13, figs 4–10.
1903 *Ampyx hornei* Etheridge & Nicholson; Reed: 19; pl. 3, figs 8–10.

LECTOTYPE. Selected herein: BM In.20829, original of Etheridge & Nicholson, 1879: pl. 13, fig. 4, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Ampyx incurvus Reed, 1906
(Pl. 3, fig. 3)

1906 *Ampyx incurvus* Reed: 161; pl. 20, figs 6–8.
1980 *Ampyx incurvus* Reed; Tripp: 133; pl. 3, figs 6, ?7.

LECTOTYPE. Selected herein: BM In.20794, original of Reed, 1906: pl. 20, fig. 7, from the Upper Balclatchie (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

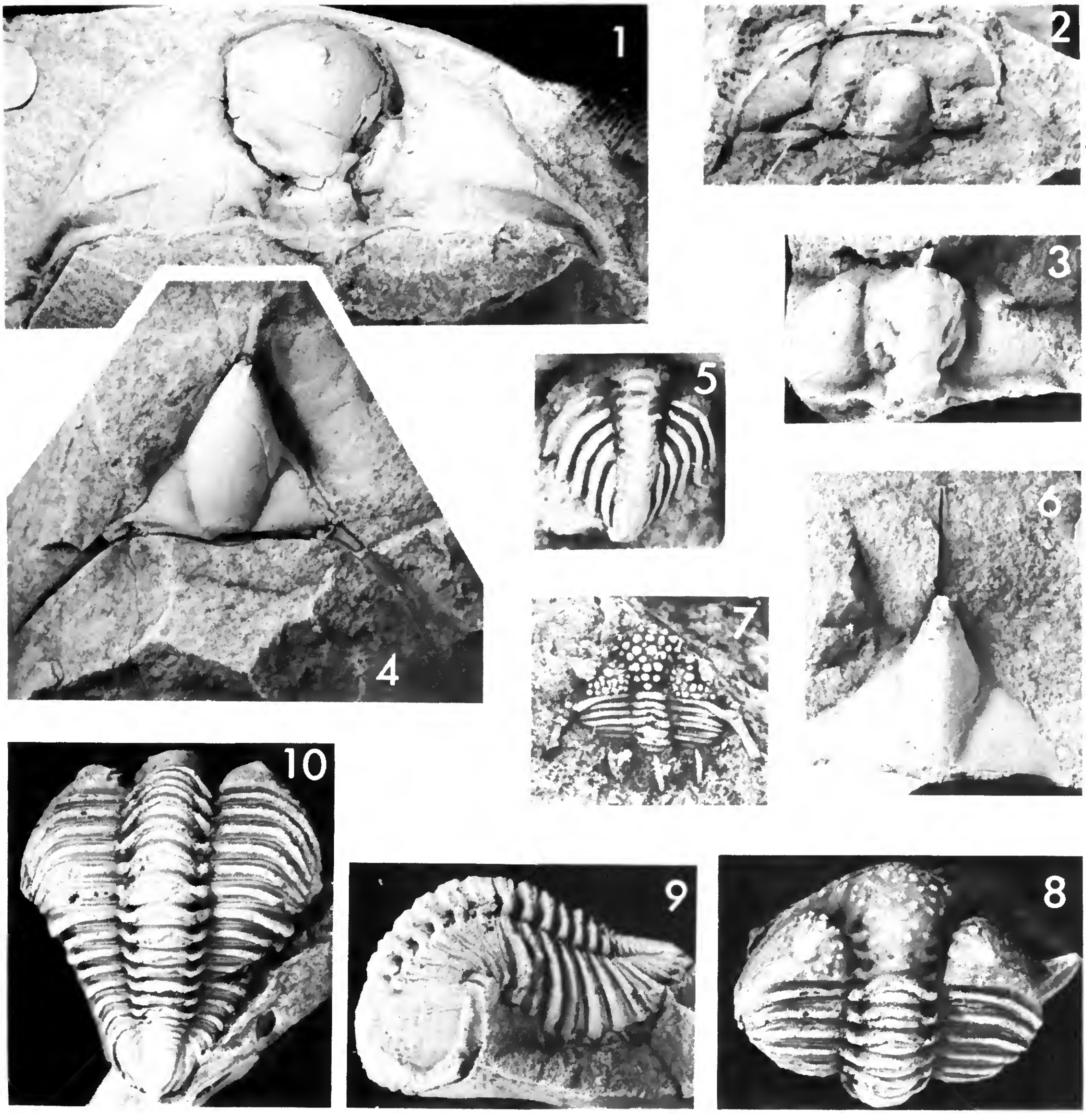

PLATE 3

Fig. 1 *Ampyx hornei* Etheridge & Nicholson, 1879, Upper Balclatchie Group, Balclatchie. Cranidium, figd Nicholson & Etheridge, 1879: pl. 13, fig. 4 and Reed, 1903: pl. 3, fig. 8. BM In.20829. × 2·2.

Fig. 2 *Otarion* (*Aulacopleura*) *reedi* (Přibyl, 1947), Upper Balclatchie Group, Balclatchie. Cephalon, figd Reed, 1906: pl. 11, fig. 14. BM In.21972. × 7.

Fig. 3 *Ampyx incurvus* Reed, 1906, Lower Ardwell Group, Ardmillan. Cranidium, figd Reed, 1906: pl. 20, fig. 7. BM In.20794. × 2·8.

Fig. 4 *Lonchodomas drummuckensis* (Reed, 1903), Ladyburn Formation, Drummuck. Figd Reed, 1903: pl. 3, fig. 1. BM In.20812. × 1·75.

Fig. 5 *Encrinuroides contentus* (Reed, 1914), Upper Balclatchie Group, Balclatchie. Pygidium, figd Reed, 1914: pl. 6, fig. 11. BM In.23231. × 2·75.

Fig. 6 *Lonchodomas macallumi* (Etheridge & Nicholson, 1879), Upper Balclatchie Group, Balclatchie. Cranidium, figd Nicholson & Etheridge, 1879: pl. 13, fig. 10. BM In.20846. × 2·8.

Fig. 7 *Erratencrinurus* (*Celtencrinurus*) *trispinosus* (Reed, 1914), South Threave Formation, Starfish Bed. Figd Reed, 1914: pl. 7, fig. 5. BM In.23225. × 2·5.

Figs 8–10 *Atractopyge michelli* (Reed, 1914), Lower Ardwell Group, Ardwell. Dorsal shield, figd Reed, 1914: pl. 7, figs 7, 7a, 7b, 7c. BM In.23310. Dorsal, left lateral and oblique posterior views, × 2.

Genus *LONCHODOMAS* Angelin, 1854

TYPE SPECIES. By subsequent designation of Vogdes, 1893: 100; *Ampyx rostratus* Sars, 1835, from the high Lower Ordovician of Huk, Norway.

Lonchodomas drummuckensis (Reed, 1903)
(Pl. 3, fig. 4)

1903 *Ampyx drummuckensis* Reed: 18; pl. 3, figs 1–5.
1931 *Ampyx (Lonchodomas) drummuckensis* Reed; Reed: 4.

LECTOTYPE. Selected herein: BM In.20812, original Reed, 1903: pl. 3, fig. 1, from the Ladyburn Formation (Rawtheyan) of Drummuck, near Girvan, Strathclyde. Grid Ref. NS 235032.

Lonchodomas macallumi (Etheridge & Nicholson, 1879)
(Pl. 3, fig. 6)

1865 *Ampyx M'Callumi* Salter: 18 (*nom. nud.*).
1879 *Ampyx macallumi* Salter; Etheridge & Nicholson: 180; pl. 13, figs 9–12.
1903 *Ampyx macallumi* Salter; Reed: 21; pl. 3, figs 11, 12.
1980 *Lonchodomas macallumi* (Salter) Tripp: 133.

LECTOTYPE. Selected herein: BM In.20846, original of Etheridge & Nicholson, 1879: pl. 13, fig. 10, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Family ENCRINURIDAE Angelin, 1854

Subfamily CYBELINAE Holliday, 1942

Genus *ATRACTOPYGE* Hawle & Corda, 1847

TYPE SPECIES. By monotypy; *Calymene verrucosa* Dalman, 1827: 100, from the Pusgill/Ashgill of Llandeilo, Dyfed, south Wales.

Atractopyge michelli (Reed, 1914)
(Pl. 3, figs 8–10)

1914 *Cybele michelli* Reed: 42; pl. 7, figs 7, 7a–c.
1935 *Cybele (Cybele) nicholsoni* Reed: 52; pl. 4, fig. 4.
1935 *Cybele (Cybele) nicholsoni*? Reed; Reed: 52; pl. 2, fig. 14.
1951 *Cybele nicholsoni* Reed; Begg: 367; pl. 1, fig. 14.
1980 *Atractopyge michelli* (Reed) Tripp: 133; pl. 4, fig. 10.

LECTOTYPE. Selected herein: BM In.23285, original of Reed, 1914: pl. 7, figs 7, 7a–c, from the Lower Ardwell Group (Caradoc) of Ardmillan Braes, near Girvan, Strathclyde. Grid Ref. NX 169938. The holotype, by monotypy, of *Cybele nicholsoni* Reed is HM A 1042, from the Lower Balclatchie Group (Caradoc) of Dow Hill, near Girvan, Strathclyde. Grid Ref. NX 190960.

REMARKS. *Cybele nicholsoni* Reed, 1935, was based upon an incomplete cranidium which is indistinguishable from *Atractopyge michelli*; we consider it to be a junior subjective synonym of the latter species.

Genus *DINDYMENE* Hawle & Corda, 1847

TYPE SPECIES. By subsequent designation of Barrande, 1852: 816; *Dindymene fridericiaugusti* Hawle & Corda, 1847, from the Králův Dvůr Formation (Ashgill) of Czechoslovakia.

Dindymene cordai Etheridge & Nicholson, 1878
(Pl. 4, fig. 5)

1878 *Dindymene cordai* Etheridge & Nicholson: 115; pl. 8, fig. 8.
1906 *Dindymene cordai* Etheridge & Nicholson; Reed: 132; pl. 17, figs 9–11.
1914 *Dindymene cordai* Etheridge & Nicholson; Reed: 44; pl. 7, figs 8, 9.

LECTOTYPE. Selected herein: BM In.23310, original of Etheridge & Nicholson, 1878: pl. 8, fig. 8 and Reed, 1906: pl. 17, fig. 10, from the Ladyburn Formation (Rawtheyan) of Drummuck, near Girvan, Strathclyde. Grid Ref. NS 235032.

Subfamily **ENCRINURINAE** Angelin, 1854

Genus ***ENCRINUROIDES*** Reed, 1931

TYPE SPECIES. By original designation; *Cybele sexcostata* Salter, 1848, from the Sholeshook Limestone Formation (Ashgill) of Sholeshook Farm, Haverfordwest, Dyfed, south Wales.

Encrinuroides contentus (Reed, 1914)
(Pl. 3, fig. 5)

1914 *Encrinurus contentus* Reed: 39; pl. 6, figs 11, 12.
1935 *Cybele* (*Cybele*?) *perversa* Reed: 53; pl. 4, fig. 5.
1980 *Encrinuroides contentus* (Reed) Tripp: 132.

LECTOTYPE. Selected herein: BM In.23231, original of Reed, 1914: pl. 6, fig. 11, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969. The holotype, by monotypy, of *Cybele perversa* Reed is HM A 1100, from the same horizon and locality.

Genus ***ERRATENCRINURUS*** Krueger, 1972

TYPE SPECIES. By original designation; '*Erratencrinurus*' *capricornu* Krueger, 1971, from the Pleistocene drift Ostseekalk, Stage E (Caradoc) of northern East Germany.

REMARKS. Krueger, 1971, erected *Erratencrinurus* without nominating a type species and therefore invalidly (Art. 36(b); I.C.Z.N. 1985: 37); the genus group name must date from Krueger, 1972 when a type species was nominated.

Subgenus ***CELTENCRINURUS*** Evitt & Tripp, 1977

TYPE SPECIES. By original designation; *Amphion multisegmentatus* Portlock, 1837, from the Killey Bridge Formation (Ashgill) of Northern Ireland.

Erratencrinurus* (*Celtencrinurus*) *trispinosus (Reed, 1914)
(Pl. 3, fig. 7)

1914 *Encrinurus multisegmentatus trispinosus* Reed: 39; pl. 7, figs 1–3.
1935 *Encrinurus multisegmentatus girvanensis* Reed: 50; pl. 4, fig. 9.
1957 *Encrinurus trispinosus* Reed; Tripp: 67; pl. 11, figs 15–19; pl. 12, figs 11–17.

LECTOTYPE. Selected herein: BM In.23225, original of Reed, 1914: pl. 7, fig. 3, from the South Threave Formation, Starfish Bed (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038. The lectotype, selected herein, of *girvanensis* Reed is HM A 1040 (= BG 963), from the same horizon and locality.

Family **CALYMENIDAE** Milne Edwards, 1840

Genus ***CALYMENE*** Brongniart, 1822

TYPE SPECIES. By original designation; *Calymene Blumenbachii* Brongniart, 1822, from the Much Wenlock Limestone Formation of Wren's Nest, Dudley, West Midlands. [I.C.Z.N. pending].

Calymene (s.l.) ***drummuckensis*** Reed, 1906
(Pl. 4, fig. 1)

1906 *Calymene blumenbachii drummuckensis* Reed: 135; pl. 17, fig. 14; pl. 18, figs 1–4.
1931 *Calymene drummuckensis* Reed; Shirley: 28; pl. 2, figs 7, 8.
1936 *Diacalymene drummuckensis* (Reed) Shirley: 400.
1977 *Calymene* (s.l.) *drummuckensis* Reed; Ingham: 101 only.

LECTOTYPE. Selected herein: BM In.23380, original of Reed, 1906: pl. 18, fig. 2, from the South Threave Formation, Starfish Bed (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038.

Family **PTERYGOMETOPIDAE** Reed, 1905

Genus *ACHATELLA* Delo, 1935

TYPE SPECIES. By original designation; *Dalmanites achates* Billings, 1860, from the Trenton Group of the City of Ottawa, Canada.

Achatella retardata (Reed, 1914)
(Pl. 4, fig. 2)

1914 *Phacops* (*Pterygometopus*) *retardatus* Reed: 49; pl. 8, figs 5–7.
1931 *Phacops* (*Pterygometopus*) *retardatus* Reed; Reed: 24.
1943 *Phacops* (*Pterygometopus*) *retardatus* Reed; Begg: 60; pl. 2, fig. 10.
1981 *Achatella retardata* (Reed) Tripp & Howells: fiches 1, 2.

LECTOTYPE. Selected herein: BM In.23603, original of Reed, 1914: pl. 8, figs 5, 5a, b, from the South Threave Formation, Starfish Bed (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038.

Genus *CALYPTAULAX* Cooper, 1930

TYPE SPECIES. By original designation; *Calyptaulax glabella* Cooper, 1930, from the Matapédia Group (Ashgill) of Percé, Quebec, Canada.

Calyptaulax asteroideus (Reed, 1914)
(Pl. 4, fig. 4)

1914 *Phacops* (*Dalmanitina*?) *asteroideus* Reed: 53; pl. 8, figs 10, 11.
1931 *Phacops* (*Calyptaulax*) *asteroideus* Reed; Reed: 24.

LECTOTYPE. Selected herein: BM In.23622, original of Reed, 1914: pl. 8, fig. 10, from the South Threave Formation, Starfish Bed (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038.

Calyptaulax hunteri (Reed, 1914)
(Pl. 4, fig. 3)

1914 *Phacops* (*Pterygometopus*) *hunteri* Reed: 52; pl. 8, figs 8, 9.
1931 *Phacops* (*Calyptaulax*) *hunteri* Reed; Reed: 24.

LECTOTYPE. Selected herein: BM In.23612, original of Reed, 1914: pl. 8, fig. 8, from the Upper Balclatchie Group (Caradoc) of Balclatchie, near Girvan, Strathclyde. Grid Ref. NX 256969.

Genus *TOXOCHASMOPS* McNamara, 1979

TYPE SPECIES. By original designation; *Trilobites extensus* Boeck, 1838, from the Caradoc of Gåsøkalven, Baerum, Norway.

Toxochasmops bisseti (Reed, 1906)
(Pl. 4, figs 7, 8)

1906 *Phacops* (*Chasmops*) *bisseti* Reed: 157; pl. 20, figs 1–3.
1931 *Phacops* (*Chasmops*) *bisseti* Reed; Reed: 25.
1981 *Toxochasmops bissetti* (Reed) Tripp & Howells: fiches 1, 2.

LECTOTYPE. Selected herein: BGSE 4368–9, original of Reed, 1906: pl. 20, figs 1, 2, from the South Threave Formation, Starfish Bed (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038.

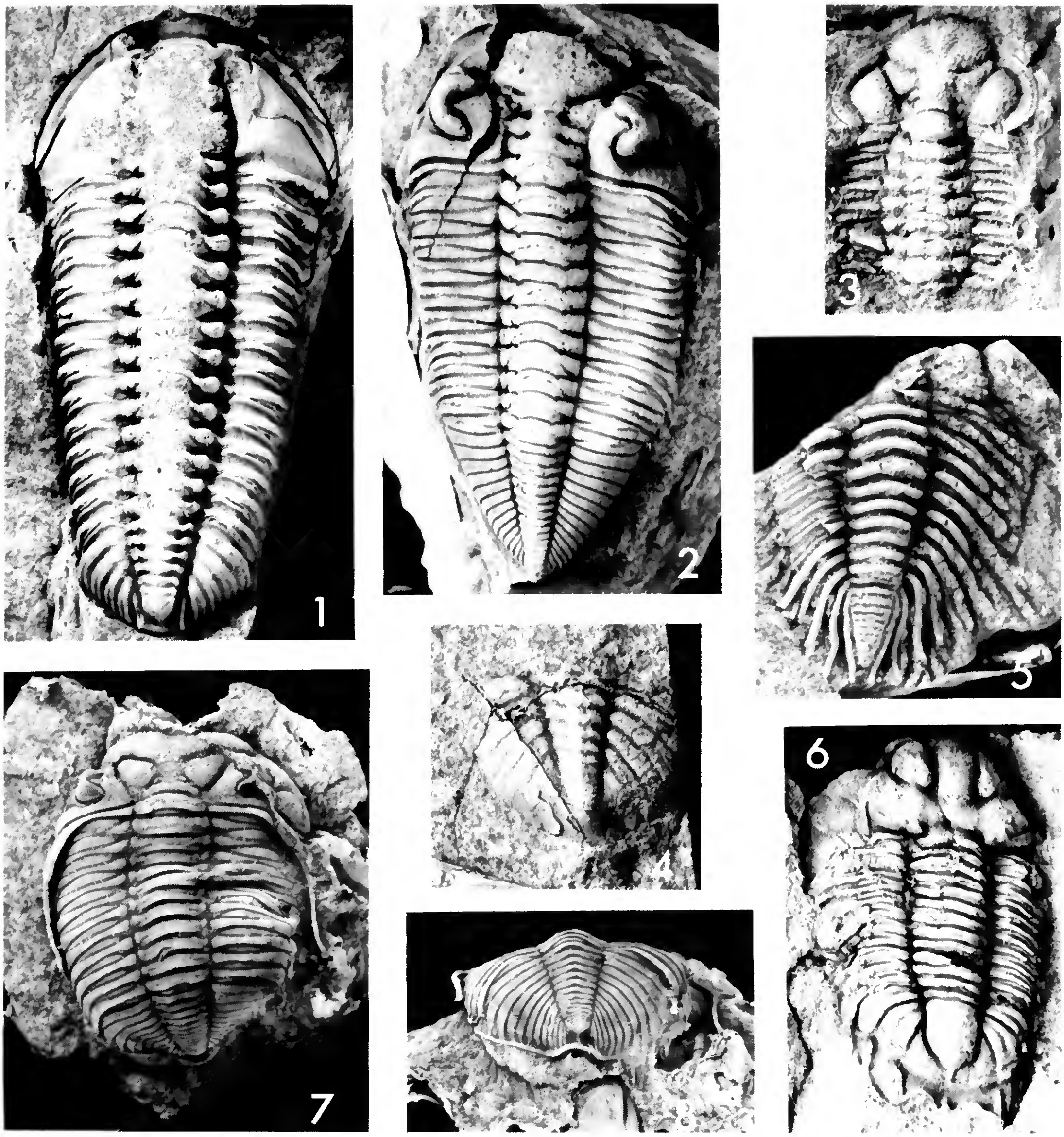

PLATE 4

Fig. 1 *Calymene* (s.l.) *drummuckensis* Reed, 1906, South Threave Formation, Starfish Bed. Dorsal shield, figd Reed, 1906: pl. 18, fig. 2. BM In.23380. × 1·1.

Fig. 2 *Achatella retardata* (Reed, 1914), South Threave Formation, Starfish Bed. Dorsal shield, figd Reed, 1914: pl. 8, figs 5, 5a, 5b. BM In.23603. × 2.

Fig. 3 *Calyptaulax hunteri* (Reed, 1914), Upper Balclatchie Group, Balclatchie. Cranidium and 7 thoracic segments, figd Reed, 1914: pl. 8, fig. 8. BM In.23612. × 3·75.

Fig. 4 *Calyptaulax asteroideus* (Reed, 1914), South Threave Formation, Starfish Bed. Pygidium, figd Reed, 1914: pl. 8, fig. 10. BM In.23622. × 2.

Fig. 5 *Dindymene cordai* Etheridge & Nicholson, 1878, Ladyburn Formation, Drummuck. Incomplete dorsal shield, figd Nicholson & Etheridge, 1878: pl. 8, fig. 8 and Reed, 1906: pl. 17, fig. 10. BM In.23310. × 3.

Fig. 6 *Hemiarges maccullochi* (Reed, 1914), South Threave Formation, Starfish Bed. Dorsal shield, figd Reed 1914: pl. 4, fig. 9. BM In.22744. × 2.

Figs 7, 8 *Toxochasmops bisseti* (Reed, 1906), South Threave Formation, Starfish Bed. Plan and posterior views of latex cast from external mould, figd Reed, 1906: pl. 20, figs 1, 2. BGSE 4368–9. × 1.

Family **LICHIDAE** Hawle & Corda, 1847

Genus ***HEMIARGES*** Gürich, 1901

Type species. By subsequent designation of Reed, 1902: 61; *Lichas* (*Arges*) *Wesenbergensis* Schmidt, 1885, from the Rakvere Limestone (Caradoc) of Estonia.

Hemiarges maccullochi (Reed, 1914)
(Pl. 4, fig. 6)

1914 *Lichas* (*Corydocephalus*) *maccullochi* Reed: 28; pl. 4, figs 9, 10.
1958 *Hemiarges maccullochi* (Reed) Tripp: 577.

Lectotype. Selected herein: BM In.22744, original of Reed, 1914: pl. 4, fig. 9, from the South Threave Formation, Starfish Bed (Rawtheyan) of South Threave Farm, near Girvan, Strathclyde. Grid Ref. NS 250038.

Remarks. This is the type species of *Choneilobarges* Phleger, 1936.

Acknowledgements

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Lower Cretaceous brachiopods from Provence, France, and their biostratigraphical distribution

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Synopsis

Articulate brachiopods from the Berriasian and Valanginian succession south of Castellane, Provence are described, including four new species: a rhynchonellid *Rhynchonella cotilloni*, a terebratuloid *Sellithyris*? *middlemissi*, and two dallinoids *Rugitela*? *rotunda* and *Advenina oweni* (type species of the new genus *Advenina*). These new species are stratigraphically distinct, and *Rhynchonella* s.s. is shown to have a representative outside of the Boreal Realm. Brachiopod speciation appears to be associated with the Lower Cretaceous marine transgressions in Provence.

Introduction

In the Lower Cretaceous sediments of the Arc of Castellane brachiopods are locally abundant. Pajaud (1974) has described brachiopods from this region which Cotillon (1971) had already found useful within a regional biostratigraphy for the Arc of Castellane. By taking transverse serial sections of duplicate material it has been possible to determine the generic affinities of some of these species. The brachiopods described here were collected from Carajuan, Point Sublime and Collet des Boules, Alpes de Haute-Provence (Figs 1–2), and also from the departments of Var and Isère, and a few specimens from near Ste Croix, Switzerland.

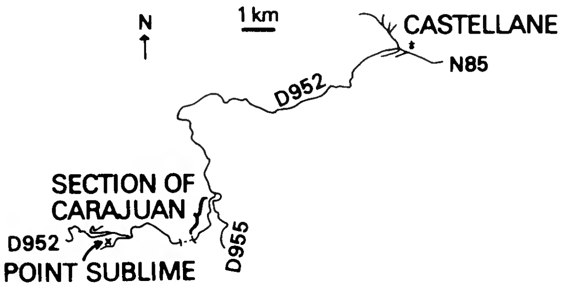

Fig. 1 Locality map for the section at Carajuan and Point Sublime, Alpes de Haute-Provence.

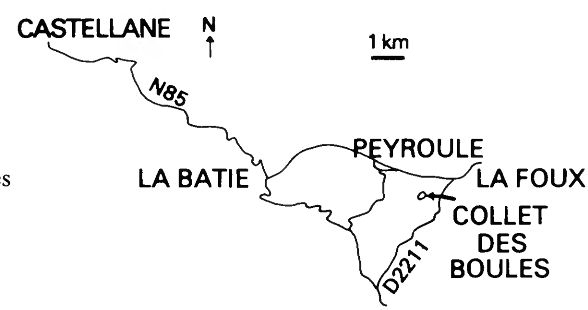

Fig. 2 Locality map for Collet des Boules, Alpes de Haute-Provence.

[1] Work undertaken in the Department of Geography and Earth Science, Queen Mary College, University of London, Mile End Road, London E1 4NS, and the Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD.

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The brachiopods are deposited in the British Museum (Natural History) unless otherwise stated (prefix BB). Material has also been available for study from the collections of Lyon, Neuchâtel and Grenoble Universities, Dr F. A. Middlemiss of Queen Mary College London, and from my own collection (prefix MS). All specimen dimensions are given in mm; L = length, W = width, T = thickness.

In the synonymies annotations follow the convention of Matthews (1973).

Stratigraphy

The succession at Carajuan, where much of the material described in this paper was collected, provides an excellent section through the Provençal facies of the Lower Cretaceous in the Arc of Castellane. This is shown in Fig. 3, based on an unpublished figure prepared for a study leaflet issued by the Pre-Albian Stages Working Group in 1979. At Carajuan the thickness of the succession from the Tithonian to the top of the Barremian is approximately 350 metres. Bed 10 of Barremian age, beds 9 and 8 ('Grande Lumachelle', L2 of Fig. 3) of Hauterivian age and bed 7 of Upper Valanginian age have not formed part of the present study. The ammonite *Saynoceras verrucosum* is found in the basal horizon of bed 7.

Bed 6, 'Petite Lumachelle' (L1 of Fig. 3) forms a hard cap to the underlying shales, and a hard-ground is developed in this yellow limestone. From this bed fifteen specimens of *Musculina sanctaecrucis* (Catzigras) were collected. The uniplicate anterior commissure, which is not typical of the species, of three of these necessitated investigation of their internal structures. Bed 6 is rich in fossils, including echinoids (*Toxaster* sp.), bivalves (including *Trigonia* sp. and *Exogyra* sp.) and gastropods.

Bed 5 comprises grey shales which yield a patchily abundant terebratellid referred to herein as *Advenina oweni* gen. et sp. nov. (p. 188). It is externally homoeomorphic with other Lower Cretaceous terebratellids but is shown to be generically distinct from them by its internal structures. At Carajuan *A. oweni* is associated with a clay-rich lithofacies and other brachiopods are uncommon. *Exogyra couloni* Defrance is recorded from this bed and may have offered a suitable substrate for the brachiopods, although the small size of *A. oweni* would assist its stability on a soft substrate. The terebratulids *Loriolithyris valdensis* (de Loriol) and *Cruralina*? *biauriculata* (d'Orbigny) are uncommon in bed 5. The echinoid *Toxaster retusus* (Lamarck) is commonly found in this bed. Beds 5 and 6 are of late Lower Valanginian age, from the ammonite evidence of beds 7 and 4. The ammonite *Saynoceras verrucosum* from bed 7 occurs 'at the very base of the late Valanginian, always in an argillaceous lithofacies probably corresponding with an important transgression' (Kemper, Rawson & Thieuloy 1981: 277).

Bed 4 consists of yellow shales and shaly limestones. The ammonite *Karakaschiceras* sp. is present in a half-metre band (K of Fig. 3), indicating a late Lower Valanginian age at Carajuan: Kemper, Rawson & Thieuloy (1981: 282) gave the age of *Karakaschiceras* as late early Valanginian to early late Valanginian.

Bed 3, alternating shales and shaly limestones with some nodular horizons, has yielded the ammonite *Thurmanniceras campylotoxus* (Uhlig), which indicates a Lower Valanginian age.

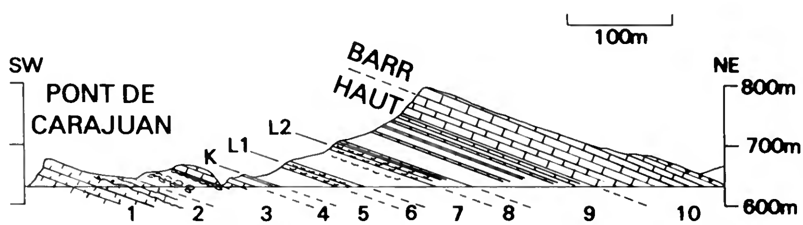


Fig. 3 The section at Carajuan, Alpes de Haute-Provence. The base line represents the course of the road D952. K = *Karakaschiceras* sp., L1 = Petite Lumachelle, L2 = Grande Lumachelle. Beds numbered 1 to 10.

Bed 2 comprises blue-grey micritic flaggy limestone, representing the start of marine sedimentation in the Lower Cretaceous. The new species *Rhynchonella cotilloni*, *Rugitela*? *rotunda* and *Sellithyris*? *middlemissi* are found in this bed, of which *R. cotilloni* was the most abundant macrofaunal element collected at Carajuan and Point Sublime. The brachiopod species from this horizon are all small, rarely greater than 1 cm in length, width or thickness. *R. cotilloni* may have been the most successful brachiopod in this environment. *Rugitela*? *rotunda* is a rare element in this fauna, only known from three specimens at Point Sublime, but present in a similar lithofacies north of Trigance, Var. Another diminutive species is represented by rare specimens of *Sellithyris*? *middlemissi*. The small size of these brachiopods may reflect winnowing from a nearby region, but the shells are well preserved and transport would have been over only a short distance. The small size of *Rhynchonella cotilloni* and *Rugitela*? *rotunda* is not confined to the sediments of Point Sublime, it is noted from other localities in Provence. This brachiopod fauna may provide an example of Cope's Rule (Cooper 1977) whereby transgressions are characterized by small forms. The ammonite *Berriasella*? gives an indication of a Berriasian age for bed 2 (M. K. Howarth, personal communication). Fragments of echinoid radiole and a belemnite (aff. *Duvalia conica* Blainville) are the only other macrofaunal elements which have been observed in my study of bed 2 at Carajuan.

At Carajuan the Tithonian white limestones (bed 1 of Fig. 3), containing nerineids, corals, echinoid radioles, bryozoa and stromatolites, are overlain by Lower Cretaceous sediments which show evidence of non-sequence at their base. In the 'calcaire blancs' facies of the uppermost Jurassic and lowermost Cretaceous of this region Cotillon (1971: 38) says it is practically impossible to delimit the Portlandian and Berriasian. The start of the Cretaceous was taken by Cotillon as thickly bedded limestones with intercalated green clays, which are found above 20–40 m of compact beds with the terebratulid *Weberithyris moravica* (Glocker) (= Tithonian).

Cotillon (1975) records the Berriasian gastropod *Ampullina leviathan* (Pictet & Campiche) from the micritic limestones of Provence (bed 2, Fig. 3). The Middle Parves Beds of the southern French Jura (Ager & Evamy 1963) also contain this Berriasian gastropod and may be the lateral equivalents of bed 2 (Fig. 3) in Provence. In the southern French Jura I have collected from the Berriasian Middle Parves Beds at Gélignieux near Belley, Ain, the brachiopods *Sellithyris carteroniana* (d'Orbigny) and *Loriolithyris valdensis* (de Loriol). These two terebratulid species confirm the Lower Cretaceous age of the Middle Parves Beds, which are in part ferruginous oolitic bioclastic limestones up to 20 m thick. This laterally discontinuous horizon may be a thicker development of the basal Cretaceous 'Unité inférieur oolithique' of Berriasian age in the Swiss Jura (Steinhauser & Charollais 1971). The latter unit includes Baumberger & Moulin's (1899) bed 5, from which they recorded two commonly occurring brachiopods, '*Terebratula*' *valdensis* and '*T.*' cf. *carteroniana*. These do not provide conclusive evidence of the Lower Cretaceous stage to which these oolitic sediments of the central Swiss and southern Jura belong as they are long-ranging species, but they do give an indication of a similar environmental setting in these areas.

The base of the Jacobi/Grandis ammonite Zone has been taken as the base of the Cretaceous and Berriasian herein (Flandrin 1975: 392).

Systematic descriptions

Order **RHYNCHONELLIDA** Kuhn, 1949

Superfamily **RHYNCHONELLACEA** Gray, 1848

Family **RHYNCHONELLIDAE** Gray, 1848

Subfamily **RHYNCHONELLINAE** Gray, 1848

EMENDED DIAGNOSIS (adapted from Ager, 1965). Shell cynocephalous to uniplicate, with strong dorsal fold. Smooth stage posteriorly, with few to many costae anteriorly, crura radulifer.

RANGE OF SUBFAMILY. Triassic to Lower Cretaceous.

Genus *RHYNCHONELLA* Fischer, 1809

TYPE SPECIES. *Rhynchonella loxiae* Fischer 1809.

EMENDED DIAGNOSIS (adapted from Ager, 1965). Small to medium in size, triangular; dorsal fold high to gently uniplicate. Costae few to numerous, usually with smooth neanic stage posteriorly. Beak small. Dental lamellae well developed, septalium shallow. Dorsal septum short or absent. Crura radulifer. Shell mosaic may be seen on internal casts.

RANGE OF GENUS. Oxfordian to Barremian.

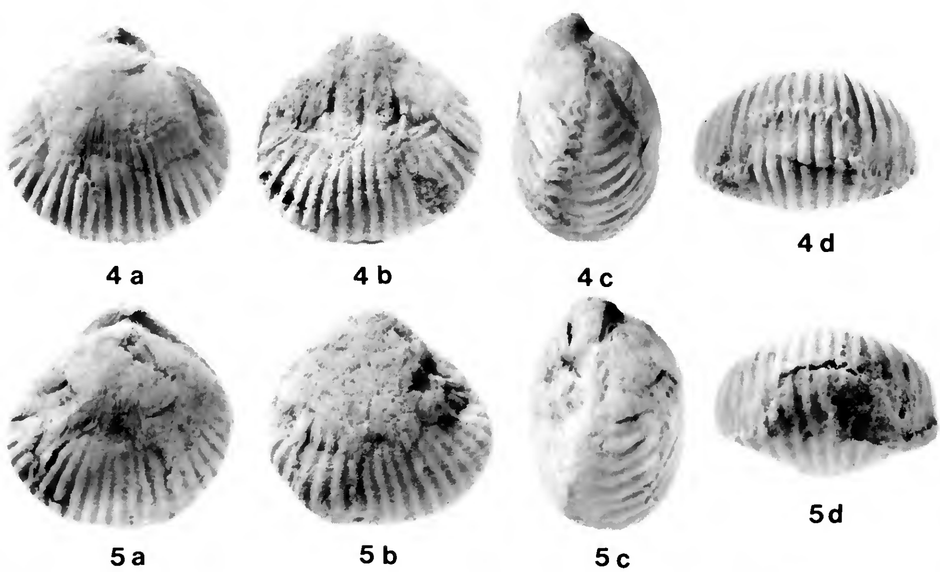
REMARKS. In a revision of the genus *Rhynchonella* s.s. Ager (1957) gave serial sections of *R. loxiae*, the type species. *R. proeminens* Yin (1931: 154; pl. XVIII, figs 12, 12a–c) was erected by Yin for one specimen from the Tithonian of Col de Ferrières, southern France. Yin's figures indicate that it has subangular costae, twelve on the brachial valve and ten (?) on the pedicle valve. There is a well-developed brachial fold with three costae on it. The pedicle umbo is suberect and there appears to be a small posteriorly smooth area on both valves. From its external characters this species appears to belong to *Rhynchonella* s.s.

Rhynchonella cotilloni sp. nov.
Figs 4–7

v? 1913 *Rhynchonella corallina* Leymerie sp. var. *neocomiensis* Jacob & Fallot: 50; pl. VI, figs 9–11; *non* figs 12–15.
non 1931 *Rhynchonella corallina* var. *neocomiensis* Jacob & Fallot; Yin: 153; pl. XVIII, figs 5–6.
1971 '*Rhynchonella*' cf. *corallina* var. *neocomiensis* Jacob & Fallot; Cotillon: 301.
1974 '*Rhynchonella*' *neocomiensis* Jacob & Fallot cf. *corallina* Leymerie; Pajaud: 96, fig. Y; pl. 1, fig. Y.

HOLOTYPE. BB82400 from the Berriasian of Point Sublime, Alpes de Haute-Provence, France. Dimensions (mm): L 10·6, W 10·9, T 7·0.

PARATYPES. BB82401–6 from the Berriasian of Carajuan, France; from bed 2 of Fig. 3. BB82407–8 from the same horizon and locality as the holotype. MS/L 1588 from the Upper Valanginian north of Trigance, Var; Lyon University Collection. Dimensions (mm): BB82401



Figs 4–5 *Rhynchonella cotilloni* sp. nov., Berriasian. Fig. 4a–d, **holotype**, BB82400; Point Sublime, Alpes de Haute-Provence. × 3. Fig. 5a–d, paratype, BB82403; Carajuan, Alpes de Haute-Provence. × 3.

L 10·5, W 10·6, T 6·8; BB82402 (sectioned; Fig. 7) L 10·4, W 10·4, T 6·6; BB82403 L 10·6, W 10·7, T 7·2; BB82404 L 10·4, W 11·6, T 7·8; BB82405 L 10·2, W 10·2, T 7·6; BB82406 L 9·5, W 9·8, T 6·7; BB82407 L 11·1, W 12·1, T 7·9; BB82408 damaged; MS/L 1588 L 11·0, W 11·4, T 7·3.

NAME. After Pierre Cotillon who has worked on the Lower Cretaceous of the Arc of Castellane.

DIAGNOSIS. *Rhynchonella* of subtriangular to subcircular outline. Width usually equal to or slightly greater than length. Maximum width just anterior of mid-length. Biconvex profile, pedicle valve flatter. Fine ribbing on both valves with smooth umbonal areas posteriorly. Uniplicate anterior commissure. Internal structures as for genus.

DESCRIPTION. The relationships between length, width and thickness are shown in Fig. 6. The brachial valve has its greatest convexity in the posterior third and anterior quarter of lateral profile. The pedicle umbo is suberect and the pedicle foramen small, circular and hypothyrid, with two small triangular deltidial plates. Beak ridges are well defined and delimit a quite wide concave interarea. The brachial valve has between 19 and 26 ribs with four to eight on the fold. The pedicle valve has between 18 and 25 ribs, with three to six in the sulcus.

The smooth area of the neanic stage covers about one-third to half of the length of both valves. This smooth area has no discernible ribs, but is covered by fine 'striae'. These are the calcite fibres of the shell, lying at an oblique angle to the shell surface, as noted by Ager (1957: 6) in *Rhynchonella loxiae* Fischer and *R. rouillieri* Eichwald, and are particularly noticeable where shell has flaked away.

Internal characters. One series of transverse serial sections is presented here (Fig. 7). The hinge plates developed horizontally and diverged anteriorly. They are only weakly deflected from the inner socket ridges (Fig. 7, section 1·6 mm). Crural base attachment is on the inner edge of the hinge plates, dorsally directed. The crura extend anteriorly as dorsomedially concave, right-angled projections and are of radulifer type (Ager 1957, 1965, 1971, Owen & Thurrell 1968).

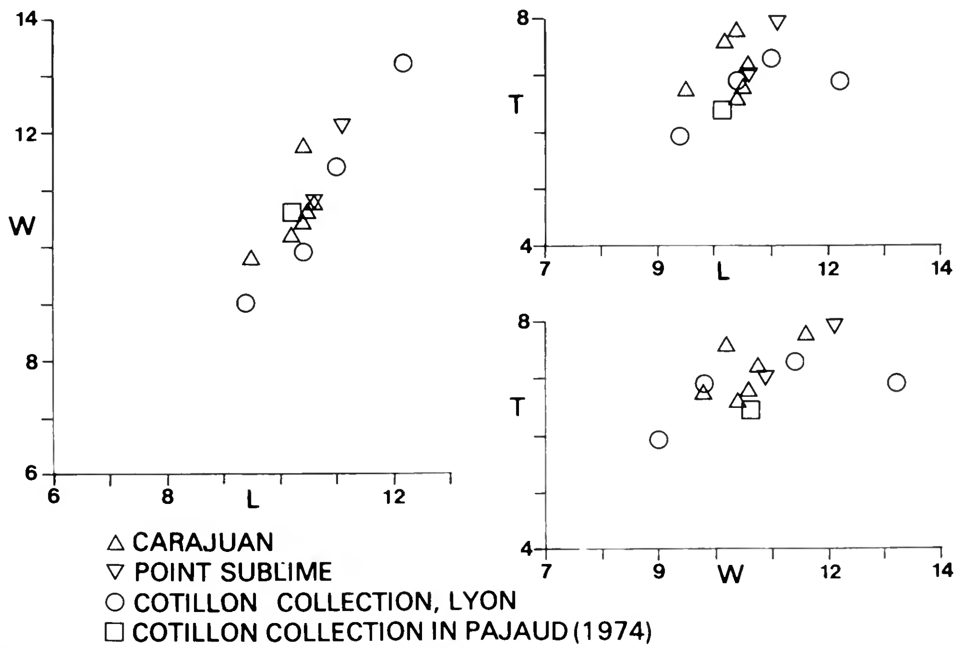


Fig. 6 Plots of Length against Width, Length against Thickness, and Width against Thickness for *Rhynchonella cotilloni* sp. nov. Dimensions in mm.

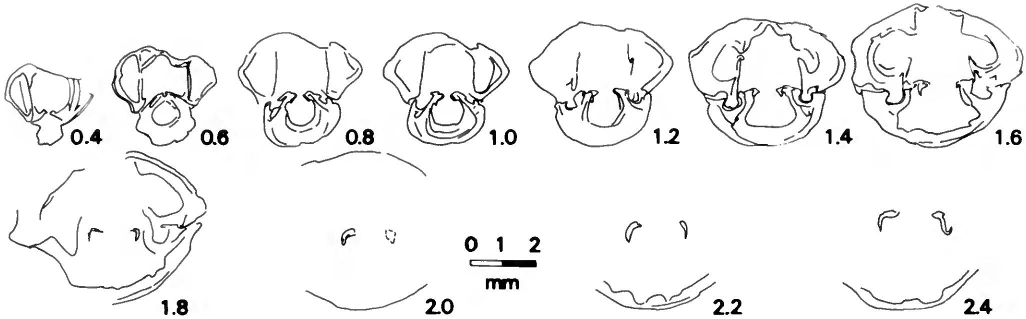


Fig. 7 Transverse serial sections through a paratype (BB82402) of *Rhynchonella cotilloni* sp. nov., Berriasian of Carajuan, Alpes de Haute-Provence. Dimensions (mm): L 10·4, W 10·4, T 6·6.

REMARKS. Jacob & Fallot (1913) gave two localities for *R. corallina* Leymerie sp. var. *neocomiensis*: Echaillon-les-Bains, Isère, and Mont Salève, Haute Savoie, France. The dimensions (mm) of three specimens from the Valanginian of Echaillon-les-Bains were given by Jacob & Fallot (1913: 50) as: L 19·0, W 19·5, T 13·0; L 20·0, W 23·8, T 12·0; L 24·0, W 24·0, T 14·0. These specimens are larger than *R. cotilloni* sp. nov.; they are also more coarsely ribbed and develop an asymmetrical anterior commissure. These specimens, figured by Jacob & Fallot (1913: pl. VI, figs 12–15) are taken as the syntypes of their var. *neocomiensis*. On the same plate (1913: pl. VI, figs 9–11) they figured material from the Berriasian of Mont Salève, immediately above the 'Purbeckian', and these are comparable in size to *R. cotilloni*. However, the latter species has finer ribbing, a large smooth area posteriorly on both valves, and a less protruding pedicle umbo.

Other rhynchonellids figured by Jacob & Fallot (1913) from the Cretaceous of south-east France closely resemble *R. cotilloni* sp. nov. *Burrirhynchia*? *gibbsiana* (Sow.) var. *sayni* Jacob & Fallot (1913: 63; pl. XI, figs 1–6, especially fig. 5) from the Barremian of Saynes, Gard, is very similar to *R. cotilloni* but has more ribs and appears to lack the smooth umbonal area present on the latter species. The juvenile specimen of '*R.*' *lata* d'Orbigny var. *minor* Jacob & Fallot (1913: 57; pl. VIII, fig. 18) from the Couche à Orbitolines du Fâ, near St Pierre-de-Chérennes, Isère, is externally similar to *R. cotilloni* in dimensions, ribbing, and its anterior fold. Burri (1956) referred this variety to *Lamellaerhynchia picteti* Burri; it has a more elongate pedicle umbo than *R. cotilloni* and has an exposed circular foramen.

R. parkhillensis Owen & Thurrell (1968) has fewer ribs than *R. cotilloni* but shares a smooth neanic stage. This latter feature has rightly been given much taxonomic significance (Ager 1965: H610 and 1971: 397).

Pajaud wrote (1974: 97) that the binomen '*Rhynchonella*' *neocomiensis* Jacob & Fallot was used for convenience for the forms from the Valanginian of Bargême, Alpes de Haute-Provence. His pl. 1, fig. Y gives a brachial view only of a specimen of the species described here as *R. cotilloni*, in which the ribbing is too fine for Jacob & Fallot's var. *neocomiensis*.

The median septum is variously developed in *Rhynchonella* s.s. and its development is incipient or lacking in *R. cotilloni*.

HORIZON AND LOCALITIES. The specimens from Carajuan were collected from bed 2 (Fig. 3), and from the same horizon at Point Sublime. Cotillon (1971) and Pajaud (1974) make no reference to the terebratulids and terebratellids associated with *R. cotilloni*, namely *Sellithyris*? *middlemissi* sp. nov. (opposite) and *Rugitela*? *rotunda* sp. nov. (p. 186). A fragment of a belemnite guard (aff. *Duvalia conica* Blainville; determined P. Doyle) was also collected at Carajuan.

Preservation of the rhynchonellids varies from complete and uncrushed to crushed and distorted; the majority of specimens appear distorted by diagenetic effects. Only a single pedicle valve has been found disarticulated.

Rhynchonella cotilloni sp. nov. is known only from the Berriasian of Provence and the Upper Valanginian of Var.

MATERIAL. From the Berriasian of Point Sublime (bed 2 of Fig. 3) four specimens, BB82400 (holotype), BB82407–8, MS 1017. Twenty specimens from the same horizon at Carajuan, MS 0165–78, including six paratypes, BB82401–6. Five specimens from the Upper Valanginian, north of Trigance, Var (Lyon University Collection), including one paratype, MS/L 1588.

Order **TEREBRATULIDA** Waagen, 1883

Suborder **TEREBRATULIDINA** Waagen, 1883

Superfamily **TEREBRATULACEA** Gray, 1840

Family **TEREBRATULIDAE** Gray, 1840

Subfamily **SELLITHYRIDINAE** Muir-Wood, 1965

Genus ***SELLITHYRIS*** Middlemiss, 1959

TYPE SPECIES. *Terebratula sella* J. de C. Sowerby 1823.

Sellithyris*? *middlemissi sp. nov.
Figs 8, 9

HOLOTYPE. BB82398, from the Berriasian of Point Sublime, Alpes de Haute-Provence. Dimensions (mm): L 14·5, W 11·9, T 7·7.

PARATYPE. BB82399 (sectioned; Fig. 9) from the same horizon and locality as the holotype. Dimensions (mm): L 12·4, W 10·0, T 6·5.

NAME. For Dr F. A. Middlemiss, who also donated the specimens.

DIAGNOSIS. *Sellithyris*? of sub-pentagonal to elongate-oval outline. Biconvex profile. Suberect pedicle umbo with short, subrounded beak ridges. Small circular mesothyrid pedicle foramen, symphytium(?) poorly developed. Lateral commissure dorsally arched, anterior commissure broadly uniplicate. Adductor muscle scars on brachial valve long, thin and parallel. Internal structures as for the genus (Middlemiss 1976: 39).

DESCRIPTION. The internal structures of one specimen have been investigated by serial sectioning (Fig. 9). The cardinal process is large, considering the small size of the specimen. The hinge plates are cuneate and ventrally concave, with small crural bases. There is a slight angular deflection of the hinge plate and inner socket ridge. The crural processes are sub-parallel.

REMARKS. The small size, lack of biplication, and relatively large adductor muscle scars suggest that these specimens are juveniles. However, the massive cardinal process is a feature usually associated with maturing or adult terebratulids.

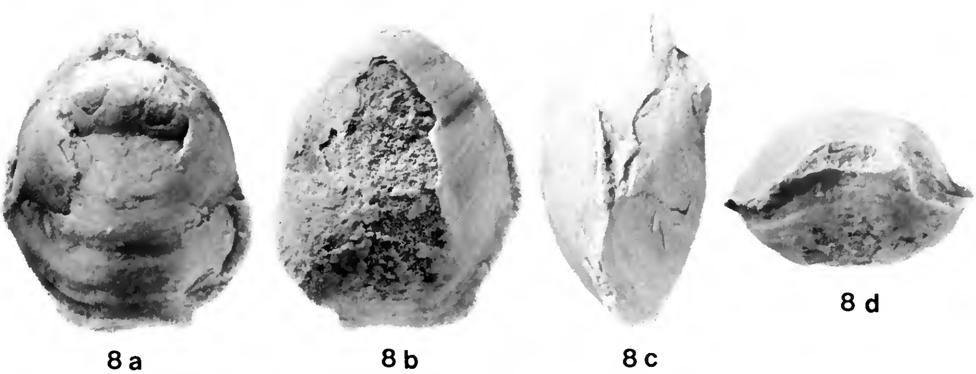


Fig. 8a–d *Sellithyris*? *middlemissi* sp. nov., Berriasian. **Holotype**, BB82398; Point Sublime, Alpes de Haute-Provence. × 3.

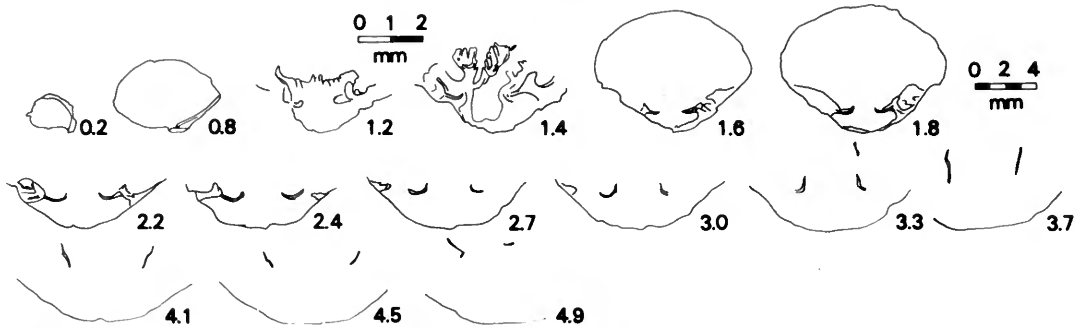


Fig. 9 Transverse serial sections through a paratype (BB82399) of *Sellithyris*? *middlemissi* sp. nov., Berriasian of Point Sublime, Alpes de Haute-Provence. Sections 1·2 mm and 1·4 mm are shown enlarged. Dimensions (mm): L 12·4, W 10·0, T 6·5.

The species appears distinct from others in the Sellithyridinae. The rounded posterior outline distinguishes it from *Loriolithyris valdensis* (de Loriol). Internally *S.*? *middlemissi* possesses a strongly developed cardinal process. It lacks the piped hinge plates as well as the initial marked deflection of the hinge plates and inner socket ridges of *Loriolithyris*. Investigation of more material of *S.*? *middlemissi* may allow a better understanding of the variability in this species.

HORIZON. Berriasian of Provence. The two specimens only.

Genus *MUSCULINA* Schuchert & Le Vene, 1929

TYPE SPECIES. *Terebratula biplicata acuta* von Buch [= *Musculina sanctaecrucis* (Catzigras, 1948)] (non *Terebratula acuta* Sowerby, 1816). Dieni, Middlemiss & Owen (1975: 181) discussed the naming of the type species.

Musculina sanctaecrucis (Catzigras)
Figs 10, 11

1834 *Terebratula biplicata acuta* von Buch: 108.
1851 *Terebratula biplicata acuta* von Buch; Quenstedt: 473; pl. 38, fig. 2 (as *T. acuta*).
v 1872 *Terebratula acuta* Quenstedt; Pictet & de Loriol: 14; pl. 202, figs 14–18.
* 1948 *Terebratula sanctae crucis* Catzigras: 391; fig. 1 (1–4, 8, 10, 12, 15–17, 19).
v 1965 *Musculina biennensis* Muir-Wood: H793; figs 658 (1), 659 (2).
v 1968 *Musculina sanctaecrucis* (Catzigras) Middlemiss: 19; fig. 9, pl. B, figs 3–4.
v 1975 *Musculina sanctaecrucis* (Catzigras); Dieni, Middlemiss & Owen: 179; pl. 32, figs 12–15.
v 1976 *Musculina sanctaecrucis* (Catzigras); Middlemiss: 53; pl. 5, figs 7–8, pl. 6, figs 1–3.

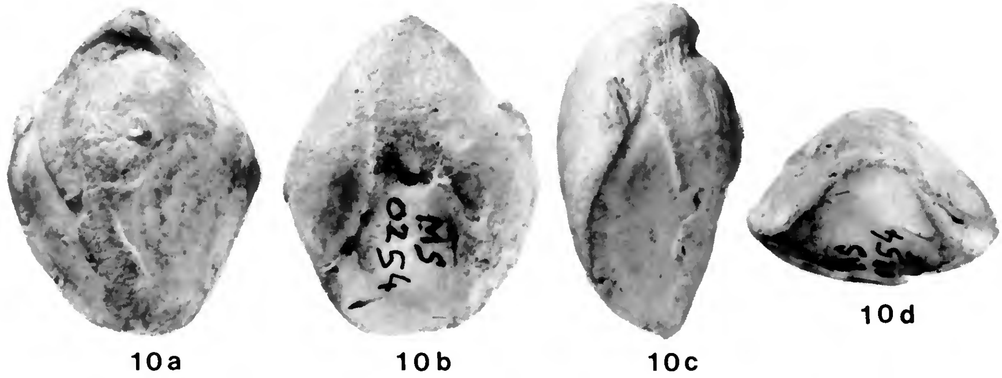


Fig. 10a–d *Musculina sanctaecrucis* (Catzigras), Lower Valanginian. Plaster cast of sectioned specimen BB86867; Carajuan, Alpes de Haute-Provence. × 3.

HOLOTYPE. The specimen figured by Quenstedt (1851: pl. 38, fig. 2) from the Neocomian of Neuchâtel, Switzerland, and preserved in the Geological-Palaeontological Institute and Museum, Tübingen (No. 48.70).

DIAGNOSIS. In the emended diagnosis of Middlemiss (1976: 52) only the following needs to be changed: 'Anterior commissure sulciplicate' emended to 'Anterior commissure rarely uniplicate to sulciplicate'.

DESCRIPTION. The species was described in detail by Middlemiss (1976). Material from the Lower Valanginian of Provence, the species' earliest known occurrence (Middlemiss 1981: 716), has been studied. From the Petite Lumachelle, Carajuan (bed 6 of Fig. 3) specimens of *M. sanctaecrucis* were collected, appearing slightly wider and thicker than specimens from the Marne d'Hauterive of the French and Swiss Jura. The pedicle umbo is more erect and the symphytium not so large in the present Provençal specimens. These distinctions may reflect stratigraphical or ecological differences.

Three specimens from Carajuan have a uniplicate anterior commissure, as opposed to the sulciplicate form typically seen in *M. sanctaecrucis*. Externally they are very similar to the sulciplicate specimens and grade into weakly biplicate forms. One of them has been serially sectioned (Fig. 11) and shows that the uniplicate specimens are variants within the limits of specific variation of the species *Musculina sanctaecrucis*. I see little point in proposing a subspecies based on three specimens that thus blend into typically sulciplicate forms.

Silicification has affected the results obtained from sectioning but the strongly concave hinge plates, clubbed crural bases, sub-parallel crural processes and the arched transverse band are typical of the genus.

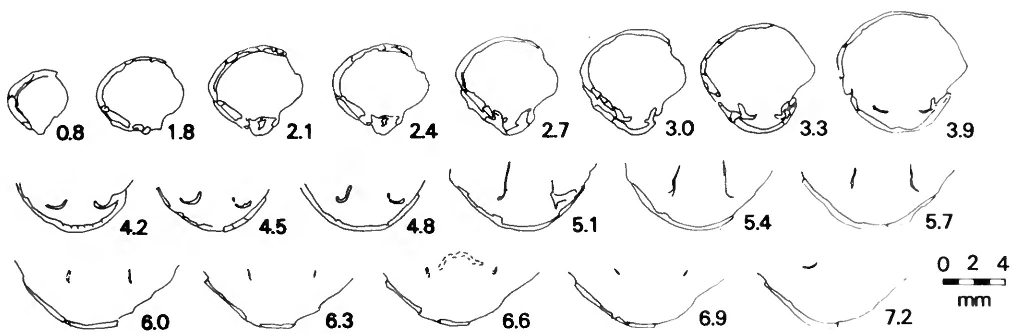


Fig. 11 Transverse serial sections through a specimen (BB86867) of *Musculina sanctaecrucis* (Catzigras); Lower Valanginian of Carajuan, Alpes de Haute-Provence. Dimensions (mm): L 15·3, W 12·2, T 8·3.

HORIZON AND LOCALITY. Bed 6 (Fig. 3), the Petite Lumachelle, Carajuan; Lower Valanginian. Middlemiss (1981: 716) gave a detailed account of this species' distribution.

MATERIAL. Fifteen complete specimens (MS 0253, MS 0255–67, BB86867 (sectioned; Fig. 11)), three with a uniplicate anterior commissure (BB86867, MS 0255–6). Nineteen fragmentary specimens (MS 0268–87).

Suborder **TEREBRATELLIDINA** Muir-Wood, 1955

Superfamily **DALLINOIDEA** Beecher, 1893

Family **DALLINIDAE** Beecher, 1893

Subfamily **DALLININAE** Beecher, 1893

Genus ***RUGITELA*** Muir-Wood, 1936

TYPE SPECIES. *Terebratula bullata* J. de C. Sowerby 1823.

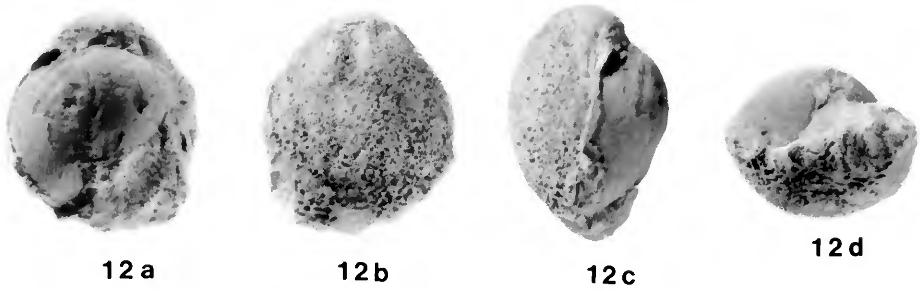


Fig. 12a–d *Rugitela*? *rotunda* sp. nov., Berriasian. **Holotype**, BB82395; Point Sublime, Alpes de Haute-Provence. × 3.

Rugitela*? *rotunda sp. nov.
Figs 12, 13

HOLOTYPE. BB82395, from the Berriasian of Point Sublime, Alpes de Haute-Provence. Dimensions (mm), including adhering matrix: L 10·5, W 9·1, T 7·4.

PARATYPES. BB82396, which has been serially sectioned, and BB82397, both from the same locality and horizon as the holotype. MS/L 1583 and MS/L 1584 from the Upper Valanginian, north of Trigance, Var, Lyon University Collection. Dimensions (mm): BB82396 L 10·9+, W 9·6, T 8·8; BB82397 L 10·0, W 9·9+, T —; MS/L 1583 L 9·4, W 8·6, T 5·7; MS/L 1584 L 8·7, W 6·9, T 6·2.

NAME. 'Rotund', referring to the shape, especially of the brachial valve in lateral and anterior profile.

DIAGNOSIS. Rotund *Rugitela*? reaching the following approximate maximum dimensions: length 11 mm, width 10 mm, and thickness 9 mm. Circular outline. Incurved pedicle umbo, pedicle foramen small, circular and mesothyrid. Short, well-marked beak ridges. Lateral commissure straight, anterior commissure rectimarginate. V-shaped septalium, crural bases triangular.

DESCRIPTION. Shell smooth. The brachial valve has a circular outline and in lateral profile is nearly semicircular, flattened slightly in the anterior half. The pedicle valve, in lateral profile, has greatest convexity posteriorly, and is somewhat flattened in the middle third of its length. The pedicle umbo is incurved, often obscuring details of the pedicle foramen and the deltidial plates. A concave interarea is defined by subrounded beak ridges. No sulcus or carina is present in either valve.

Internal characters. The internal structures of one specimen have been investigated by serial sectioning (Fig. 13). The dental lamellae are weak and the pedicle collar has attached to it a

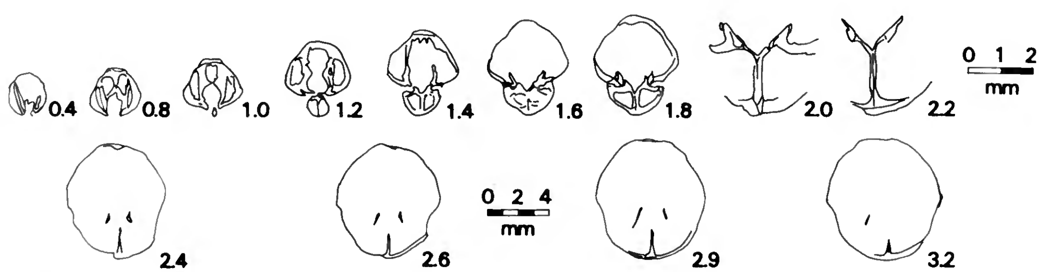


Fig. 13 Transverse serial sections through a paratype (BB82396) of *Rugitela*? *rotunda* sp. nov., Berriasian of Point Sublime, Alpes de Haute-Provence. Sections 2·0 mm and 2·2 mm are drawn at a larger scale. Dimensions (mm): L 10·9+, W 9·6, T 8·8.

small ventral septum (section 0·8 mm). A well-developed V-shaped septalium is supported by a median septum. The inner socket ridges are not deflected from the hinge plates. Anteriorly the median septum, hinge plates and crural bases form a Y-shaped outline (2·2 mm). The septalium is most acute in this section, and the wedge-shaped crural bases taper ventrally. The free crural bases are medially convex and the crural processes converge ventrally. The median septum was traced to section 4·2 mm.

REMARKS. Externally this species is very similar to the Jurassic brachiopods *Rugitela bullata* (J. de C. Sowerby) and the terebratulid genus *Sphaeroidothyris* Buckman. *R.*? *rotunda* can be distinguished from *Sphaeroidothyris* by its incurved pedicle umbo and the presence of a median septum and dental lamellae, often conspicuous by external examination. *R.*? *rotunda* is not known to have reached the dimensions of *R. bullata*. A sulcus is not developed in *R.*? *rotunda*, whilst in *R. bullata* it may give rise to ligate folding.

The evidence of internal structures only allows a provisional assignment to *Rugitela*. The thickening around the pedicle umbo and the presence of a small ventral septum is shared with other Lower Cretaceous genera, for example *Zittelina* Rollier. Muir-Wood's (1936: fig. 32) sections of *R. bullata* show thickening in the pedicle umbo. *R.*? *rotunda* has a wide and quite deep V-shaped septalium. The angle of the septalium is quite acute, comparable to that seen in *Zittelina wahlenbergi* (Zejszner) figured by Barczyk (1971: fig. 1). The typical W-shaped hinge plate configuration of *Rugitela* s.s. is not seen in *rotunda*, but both share medially convex, free crural bases which expand anteriorly and a persistent median septum. The lack of a median ridge in the septalium of *R.*? *rotunda* could be because of immaturity in the sectioned specimen. The septalium is similar to that seen in *Dzirulina*, but the wedge-shaped, ventrally pointing crural bases and their subsequent anterior development differ from that genus.

In *Advenina* gen. nov. (p. 188) the hinge plates are subhoriazontal within the septalium. The acute septalium and more strongly developed dental lamellae of *R.*? *rotunda* help distinguish it from *A. oweni* sp. nov.

R.? *rotunda* can be distinguished from the similar-sized terebratellid *Hynniphoria globularis* Suess (1859) by its biconvexity of both valves, especially of the brachial valve, lack of the sulcate neanic shell seen in Suess' species and its characteristically well-marked shell endopunctation. The dental lamellae in the pedicle valve of *H. globularis* are seen to diverge at about 90° when viewed ventrally, whilst in *R.*? *rotunda* they diverge at about 30°.

Dagys (1968) figured and sectioned a globose 'bubble-like' terebratellid from the Lower Volgian of Siberia, which he referred to *Russiella bullata* (Rouillier). The figured specimens are larger than any of *R.*? *rotunda* seen to date, and in profile lack the globosity of the brachial valve. In Dagys' material the brachial valve is somewhat flattened, whereas the pedicle valve is more convex than that of *R.*? *rotunda*. Internally it has a gently convex septalium from which the descending branches project anteriorly from the lateral edges.

The globose external morphology of *Rugitela*? *rotunda* is reminiscent of *R. bullata* (J. de C. Sowerby) of the Jurassic, but no direct link is inferred. Internally the features of *R.*? *rotunda* are comparable to *Rugitela*, but they are not typical.

HORIZON. Berriasian of Provence (bed 2, Fig. 3) and Upper Valanginian of Var.

MATERIALS AND LOCALITIES. Three specimens from Point Sublime, Alpes de Haute-Provence, BB82395–7. Four specimens from north of Trigance, Var (Lyon University Collection), MS/L 1583–6.

Genus *ADVENINA* gen. nov.

TYPE SPECIES. *Advenina oweni* sp. nov.

NAME. From *advena*, 'newcomer'.

DIAGNOSIS. Oval, sub-pentagonal or sub-triangular in outline. Biconvex profile, smooth-shelled. Pedicle umbo erect, foramen of medium size, circular, mesothyrid. Deltidial plates disjunct or conjunct, may be obscured. Beak ridges sharp, defining broad interarea. Anterior commissure rectimarginate to uniplicate, crenulation may be developed. Lateral commissure straight.

Internal characters. Dental lamellae weakly developed. Septalium is well developed, acute posteriorly, anteriorly broadens and shallows, and is supported by a median septum. Septalium and median septum give Y-shaped outline in transverse section. Crural bases are given off at lateral edges of the septalium, closely associated with thickened inner socket ridges. Crural bases taper, giving a wedge shape in transverse section. Median septum persists anteriorly beyond the septalium and may extend to half total valve length or beyond. Crura stout, but rapidly extend into high crural processes. Remaining descending and ascending branches thin.

SPECIES INCLUDED. *Advenina oweni* sp. nov. Other specimens of *Advenina* have been described by Lobacheva (1966) under the names *Psilothyris tamarindus* (Sowerby), ?*P.* (?) *kouensis* (Moisseev) and *P.* aff. *favrei* (de Loriol).

RANGE OF GENUS. Berriasian?; Valanginian–Barremian.

REMARKS. *Advenina* is externally homoeomorphic with a number of Mesozoic terebratellids but can be distinguished by its internal structures. In *Advenina* the hinge plates are anteriorly sub-horizontal within the septalium. The acute septalium, more strongly developed dental lamellae and secondary callus thickening in the pedicle umbo of *Rugitela*? *rotunda* (p. 186) help to distinguish it from *A. oweni.*

The genus *Advenina* is proposed for brachiopods described from faunas of Tethyan and Jura affinities, associated with clay-rich sediments (in France and Switzerland), as are specimens of *Rugitela* (Owen 1973: 128). Lobacheva (1966) records specimens, referred herein to *Advenina*, from the Valanginian to Aptian of the Kopet Daga, although material of Hauterivian to Aptian age referable to *Advenina* has not been found in western Europe.

Internally *Advenina* lacks the median ridge which is often strongly developed in the septalium of *Rugitela*, and has not been seen to possess the secondary callus thickening in the pedicle umbo often present in the latter genus. The anterior commissure of *Rugitela* is sulcate or rectimarginate; in *Advenina* it is rectimarginate to uniplicate. In *Rugitela* the crural bases are given off dorsally, which, in conjunction with the median ridge, give rise to the W-shaped septalium, which is well developed in this genus. In *Advenina* the crural bases are given off at the lateral edges of the septalium producing a Y shape when the septalial plates, crural bases and median septum are still in contact, as seen in transverse section.

Advenina can be distinguished from the externally homoeomorphic genus *Dzirulina* Noutsoubidze 1945 by its internal structures. Externally both genera are circular in outline with an evenly biconvex profile, suberect pedicle umbo and circular mesothyrid (to permesothyrid) pedicle foramen. Incipient uniplication may be developed. Internally the two genera share weak dental lamellae, but the septalium is broader and flatter in *Dzirulina*. The acute Y shape of the ascending branches attached to the septal pillar in *Dzirulina* distinguishes it from *Advenina* where no attachment is seen.

Advenina oweni sp. nov.
Figs 14–18

1971 *Rugitella hippopus* (Roemer) (*sic*); Cotillon: 29.
1974 *Rugitela hippopus* (Roemer); Pajaud: 100, fig. D; pl. 2, fig. D.
1979 *Rugitela tamerindus* (Sowerby) (*sic*); Richter: 113; fig. 121.

HOLOTYPE. BB86852, from the Lower Valanginian of Carajuan, Alpes de Haute-Provence; from bed 5 of Fig. 3. The specimen measures (mm): L 14·5, W 12·5, T 8·6.

PARATYPES. BB86853–8 from the same locality and horizon as the holotype. BB86859 from the Lower Valanginian of Collet des Boules, south-east of Peyroules, Alpes de Haute-Provence. MS/L 1579 from the Valanginian of La Treille, Var; Lyon University Collection. Dimensions (mm): BB86853 L 13·4, W 11·7, T 8·2; BB86854 L 15·1, W 12·2, T 8·7; BB86855 (sectioned; Fig. 16) L 5·3, W 4·3, T 2·8; BB86856 L 9·9, W 8·6, T 6·2; BB86857 L 12·5, W 10·5, T 8·0; BB86858 (sectioned; Fig. 17) L 14·0, W 11·6, T 9·3; BB86859 (sectioned; Fig. 18) L 13·5, W 11·8, T 8·8; MS/L 1579 L 11·5, W 9·6, T 7·7.

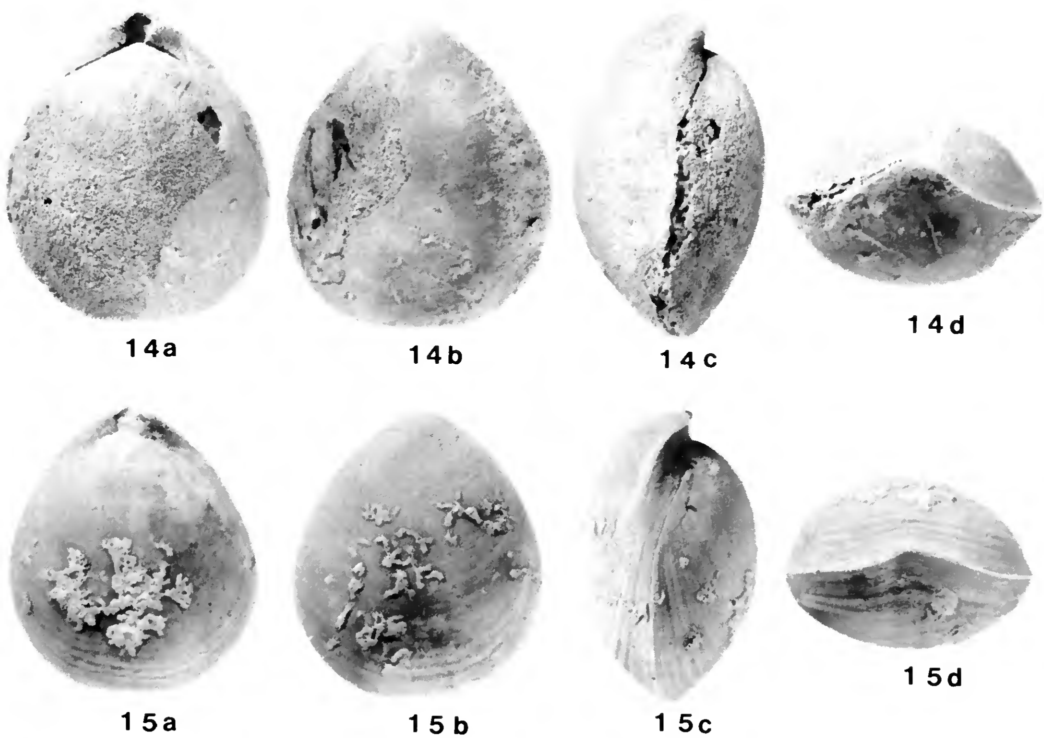
NAME. After Dr E. F. Owen.

DIAGNOSIS. *Advenina* typically sub-triangular, from elongate-oval to sub-quadrate in outline. Maximum width in anterior half of shell. Anterior commissure narrowly uniplicate. Septalium U- to V-shaped. Persistent median septum, thickened crural bases given off ventrally.

DESCRIPTION. Pedicle umbo suberect, often broken to expose dental lamellae. Pedicle foramen of medium size, circular, mesothyrid, with beak ridges that border a quite wide concave inter-area. Deltidial plates small, rarely visible. The anterior margin of the shell outline is straight-truncate to rounded, and may appear incipiently bilobate when the uniplication of the brachial valve has been slightly crushed. In the anterior third of the pedicle valve a narrow sulcus, about one-third of the valve's width or less, is developed. This is bordered by carinae. The sulcus may persist for two-thirds of the length of the pedicle valve from the anterior commissure. The pedicle sulcus is developed as a narrow, weak, dorsal uniplication of the anterior commissure, which may be 'pointed'. There is no distinct fold in the brachial valve anteriorly. Punctation is well marked and growth lines are faint, although in a few specimens they are well marked.

Internal characters. Serial sections of three specimens are presented here. Fig. 16 shows a series of serial sections taken from the smallest available for study, which measured (mm): L 5·3, W 4·3, T 2·8. The septalium is well developed at this early growth stage and is anteriorly supported by the median septum (1·4 mm). The crura are given off from the ventral edge of the hinge plates. The transverse band is dorsally concave. The median septum is long, increasing in height anteriorly (2·3 mm), and with the close proximity of the transverse band (2·5 mm) this suggests the campagiform phase had already been passed through, and that resorption of the hood had taken place.

An adult of *A. oweni* is represented by the series of sections in Fig. 17. The septalium widens anteriorly and the hinge plates become more horizontal too. The transverse band is not observed but the ascending branches are well preserved (6·8 mm).



Figs 14–15 *Advenina oweni* gen. et sp. nov., Lower Valanginian of Carajuan, Alpes de Haute-Provence. Fig. 14a–d, **holotype**, BB86852. × 3. Fig. 15a–d, paratype, BB86853. × 3.

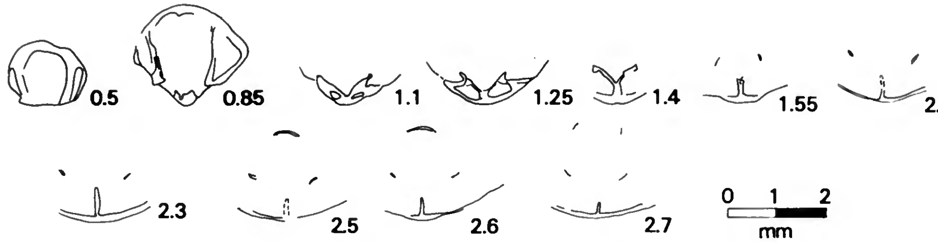


Fig. 16 Transverse serial sections through a juvenile paratype (BB86855) of *Advenina oweni* gen. et sp. nov.; Lower Valanginian of Carajuan, Alpes de Haute-Provence. Dimensions (mm): L 5·3, W 4·3, T 2·8.

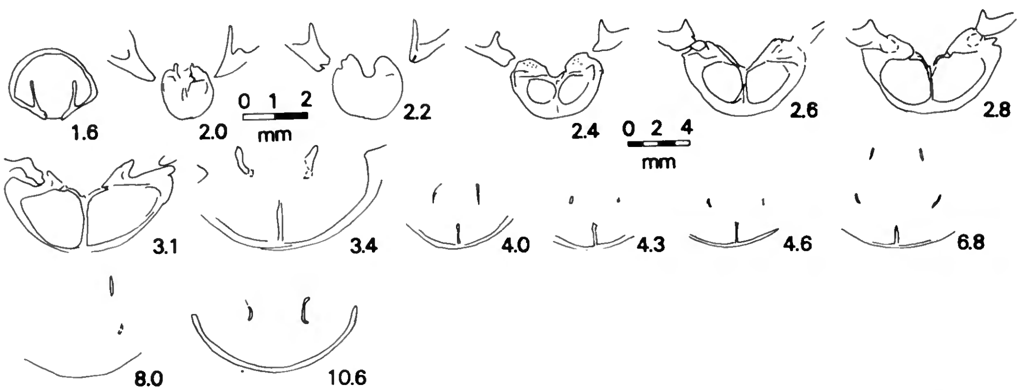


Fig. 17 Transverse serial sections through an adult paratype (BB86858) of *Advenina oweni* gen. et sp. nov.; Lower Valanginian of Carajuan, Alpes de Haute-Provence. Sections 2·0 mm to 3·4 mm are drawn at a larger scale. Dimensions (mm): L 14·0, W 11·6, T 9·3.

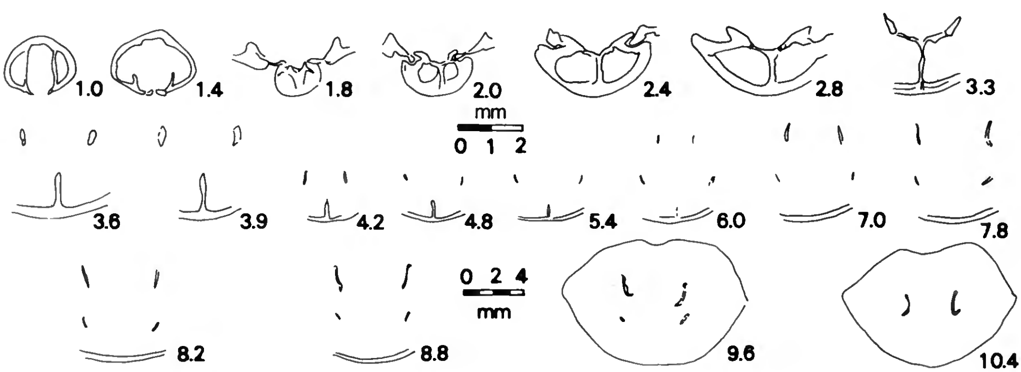


Fig. 18 Transverse serial sections through an adult paratype (BB86859) of *Advenina oweni* gen. et sp. nov.; Lower Valanginian of Collet des Boules, Alpes de Haute-Provence. Sections 1·8 mm to 3·9 mm are drawn at a larger scale. Dimensions (mm): L 13·5, W 11·8, T 8·8.

Fig. 18 shows a series of sections of an adult specimen of *A. oweni* from Collet des Boules. This shows the septalium very clearly, and the thickened shell in the vicinity of the inner socket ridge and socket floor. Anteriorly the crura develop near these thick inner socket ridges (3·3 mm) and the sub-horizontal hinge plates are well displayed. The descending branches curve laterodorsally and the ascending branches are sub-parallel.

No terminal or lateral spines have been observed on the descending branches on any of the

sectioned specimens. As these are fragile structures it is possible that they are not always preserved or they may be difficult to differentiate from the matrix.

REMARKS. Serial sections given by Lobacheva (1966: figs 23, 24) of specimens from the Hauterivian to Aptian of the Crimea, northern Caucasus, Georgia and Kopet Daga share a number of similarities with *A. oweni*. These specimens all share weak dental lamellae, and a broad, fairly shallow septalium lacking a median ridge, which is supported by a fairly persistent median septum. *A.* aff. *favrei* as figured by Lobacheva (1966: fig. 24) has an unusual development of the median septum, in that it splits into a dorsal and ventral component anteriorly and is then lost. This is seen as reflecting greater resorption of the septum in an adult (loop traced to 12·9 mm), but the septum is present again anteriorly, implying this is the site of former attachment of the hood. The crural processes are high (section 4·5 mm), comparable to those seen in *A.* aff. *oweni* (Fig. 20, section 4·1 mm), except that in *A.* aff. *favrei* the median septum has been resorbed.

A. oweni has a close resemblance externally to *Psilothyris tamarinda* (J. de C. Sowerby), but the former species has a more triangular outline (due to its more anterior maximum width) and also has a narrower sulcus in the pedicle valve. *A. oweni* differs from *P. occidentalis* Cooper by the more inflated profile of its brachial valve and its sub-triangular outline. Work in progress on *P. occidentalis* suggests that *Tamarella* Owen 1965 is a junior subjective synonym of *Psilothyris* Cooper 1955. *A. oweni* does not develop the elongation of the valves at the site of the uniplication seen in ?*P. ullukolensis* (Moisseev) shown by Smirnova (1972). The latter species also has a wider and stronger uniplication, and a less inflated profile.

A. tamarindus, as shown by Lobacheva (1966), has a more circular outline than *A. oweni*. *Dzirulina favrei* (de Loriol) has its maximum width of outline more posteriorly placed than in *A. oweni*, and does not possess the uniplication typically developed in the latter species.

D. pseudojurensis (Leymerie) has a wider uniplication of the anterior commissure than that of *A. oweni*, and it lacks the bordering carinae. *A. oweni* has a convex pedicle valve and poorly exposed deltidial plates, and lacks the sub-pentagonal outline of *D. pseudojurensis*. *A. oweni* may rarely be cinctiform in outline, but this is usually owing to crushing of the anterior commissure, emphasizing the weak pedicle sulcus. There are, however, specimens of *A. oweni* which closely resemble *D. pseudojurensis* externally, and these have yet to be investigated internally.

D. regularis (Smirnova), from the Lower Hauterivian of the Crimea, appears more pentagonal in outline than *A. oweni* and has a rectimarginate anterior commissure. These comments also apply to the Lower Barremian *D. marianovkensis* (Moisseev) as shown by Smirnova (1972). *D. plana* (Smirnova) from the Barremian to Aptian of the northern Caucasus has a more cinctiform outline with more anterior maximum width, tends to have a less inflated brachial valve and lacks the uniplication of *A. oweni*. *D. haughtoni* Owen from the Upper Aptian of northern Zululand has a more circular outline than *A. oweni* and is incipiently uniplicate. The above species referred to *Psilothyris* and *Dzirulina* may also be distinguished from *A. oweni* by their internal structures. However, Smirnova (1972) only presented serial sections of one of the species now referred to *Dzirulina*, namely *D. plana* (Smirnova), the type species of her now invalid genus *Belothyris*.

Pajaud (1974: pl. 2, fig. D) figured a Lower Cretaceous brachiopod from Provence and referred it to *Rugitela hippopus* (Roemer). This specimen is now recognized as *Advenina oweni* sp. nov. The most striking difference externally is that *R. hippopus* is sulcate, whereas *A. oweni* is uniplicate.

HORIZON AND LOCALITIES. Lower Valanginian, Carajuan and Collet des Boules, south-east of Peyroules, Alpes de Haute-Provence (bed 5 of Fig. 3). Upper Valanginian of La Treille, Var. Berriasian? of Sarcenas, Isère, Grenoble University Collection. Pajaud (1974) records this species as *Rugitela hippopus* from the Upper Valanginian of La Martre-Châteauvieux, Var.

MATERIAL. Over two hundred specimens from Carajuan, including the holotype and six paratypes (BB86852–8). One hundred and thirty-seven specimens from Collet des Boules, including one paratype (BB86859). Two hundred and fifty-eight specimens from La Treille (Lyon University Collection), including one paratype (MS/L 1579).

Advenina aff. ***oweni*** sp. nov.
Figs 19, 20

REMARKS. In the collection of Neuchâtel University are five brachiopods referred to *A.* aff. *oweni.* The specimens are of Valanginian age, from Le Collaz, Ste Croix, Switzerland, from the Bourquin Collection. *A.* aff. *oweni* appears to be more variable than *A. oweni* from Provence. However, this may reflect the scarcity of specimens of *A.* aff. *oweni* from Le Collaz compared to the numerous specimens of *A. oweni* from Provence where morphologically intermediate forms link variants, showing the variability to be within one species. The Swiss specimens are subtriangular, with a similar lateral profile to the French material, and beak characteristics are comparable. One specimen (MS/N 1594) has an unusually highly inflated brachial valve posteriorly, but they all possess a uniplicate anterior commissure.

An interesting development of the anterior commissure is seen on the specimen of *A.* aff. *oweni* that has been serially sectioned (MS/N 1065). Small and very short crenulate folds are developed on the uniplication. This feature was also noted by de Loriol (1896) on '*Zeilleria*' *favrei*, who commented on it as being a very variable feature. This crenulation is apparently rarely developed, although it would seem to be more common at Le Collaz among the few specimens as yet available.

The crenulation of the anterior commissure is an unusual feature among terebratelloids and its development must remain somewhat conjectural. It is known in *Dzirulina favrei* (de Loriol), and in ?*A. kouensis* (Moisseev) and *A.* aff. *favrei* both shown by Lobacheva, as well as in *A.* aff. *oweni.* Pictet & de Loriol (1872: 70) recorded some specimens of the terebratulid *Loriolithyris russillensis* (de Loriol) from the Valanginian limonite of Villers-le-Lac with multiple folds of the anterior commissure. This is comparable to the crenulation of the anterior commissure seen in the present form from the Valanginian of Le Collaz, but the crenulation is confined to the commissure in the latter species and not developed as discrete folds as in *L. russillensis* (Pictet & de Loriol 1872: pl. 202, fig. 6a–c). However, its development may be related to environmental conditions.

The matrix on and infilling the specimens of *A.* aff. *oweni* is a micritic limestone that has given a yellow-orange staining to parts of some specimens, showing it to be ferruginous, but more detailed information on the lithology from which they were collected is not available. Sedimentological information is also lacking for the forms described by de Loriol (1896) as '*Zeilleria*' *favrei*, from the Lower Cretaceous of the Crimea, in which crenulation is developed on a rectimarginate to incipiently uniplicate anterior commissure. Crenulation in terebratellids is associated with maturity and is asymmetrically developed. If its formation were an adaptation for the exclusion of larger particles it might have developed earlier in growth, as this would be a constant requirement throughout life; in any case the crenulation is developed in what is generally accepted as the 'exhalent' part of the anterior commissure. The crenulation would have increased the surface area of the mantle epithelium, and this might have aided oxygen, or

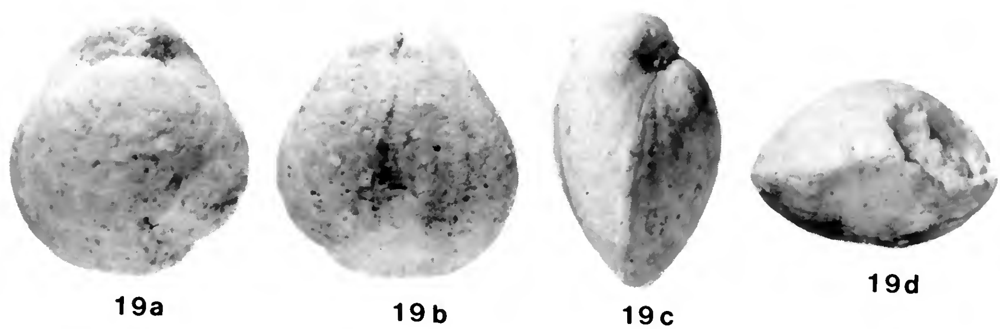


Fig. 19a–d *Advenina* aff. *oweni* gen. et sp. nov., Valanginian. Plaster cast of sectioned specimen from Neuchâtel Collection, MS/N 1065; Le Collaz, Ste Croix, Switzerland. × 3.

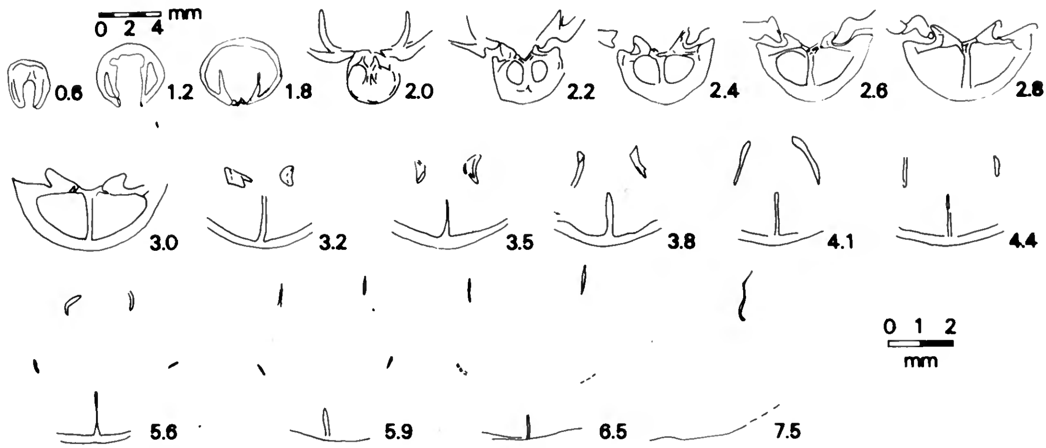


Fig. 20 Transverse serial sections through a specimen (Neuchâtel Collection, MS/N 1065) of *Advenina* aff. *oweni*; Valanginian of Le Collaz, Ste Croix, Switzerland. Sections 0·6 mm to 1·8 mm are drawn at a smaller scale. Dimensions (mm): L 12·5, W 11·1, T 8·0.

nutrient, assimilation. Crenulate *Loriolithyris russillensis* and *Advenina* aff. *oweni* both appear to be associated with iron-bearing sediments.

Internal characters. One specimen of *A.* aff. *oweni* was serially sectioned to determine its relationship to the Provençal material. Internally the specimen has weakly developed dental lamellae and an initially acute septalium which becomes wider and shallower anteriorly. The inner socket ridges and hinge plates form a wedge-shaped outline, tapering towards the median septum (Fig. 20, section 2·8 mm). The crura are more strongly medially convex than those seen in the French specimens of *A. oweni.* The crural processes are quite high (4·1 mm). The configuration of the descending branches is similar to that seen in *A. oweni* (Fig. 18). The median septum is persistent and is slightly swollen on its ventral edge in sections 4·1 and 4·4 mm, possibly indicating a site of former hood attachment, comparable to section 4·0 mm of Fig. 17.

HORIZON AND LOCALITY. *Advenina* aff. *oweni* is recorded from the Valanginian of Le Collaz, Ste Croix, Switzerland.

MATERIAL. Five specimens from Le Collaz; Bourquin Collection, Neuchâtel University. Specimen numbers MS/N 1065 (sectioned; Fig. 20), MS/N 1592–5.

Conclusions

In Europe the migration of brachiopods from platform areas, for example the Jura, to continental margins (sub-Tethyan, that is, between Jura Platform and deeper water Tethyan facies) is believed to be the response of these benthonic organisms to the end-Jurassic regression, leading to a polarization of Tethyan and Boreal brachiopod faunas during the Tithonian and Berriasian. *Rhynchonella, Rugitela* and *Ornithella* are associated with clay-rich sediments and have a Boreal distribution, whilst *Lacunosella* and *Zittelina* occur in micrites and *Juralina* and *Weberithyris* in peri-reefal and reefal limestones of the Tethyan realm. *R. cotilloni* is a Lower Cretaceous exception for the genus by occurring in Tethyan micritic limestones. *Ornithella farquharsoni* (Muir-Wood, 1935) from the Lower to Middle Kimmeridgian of Somalia shows this genus to be widespread. and the Lower Cretaceous genus *Advenina* described from Tethys and the Jura may be derived from the dominantly Boreal genus *Rugitela.*

Thomson & Owen (1979: 35) stated 'It is clear that several "Northern Hemisphere" genera are more widely distributed than previously appreciated . . .' and the occurrence of *Rhynchonella cotilloni* in Provence would tend to confirm this. *Rhynchonella proeminens* Yin is tentatively referred to *R.* s.s., this Tithonian species thus providing a link with the Boreal Portlandian

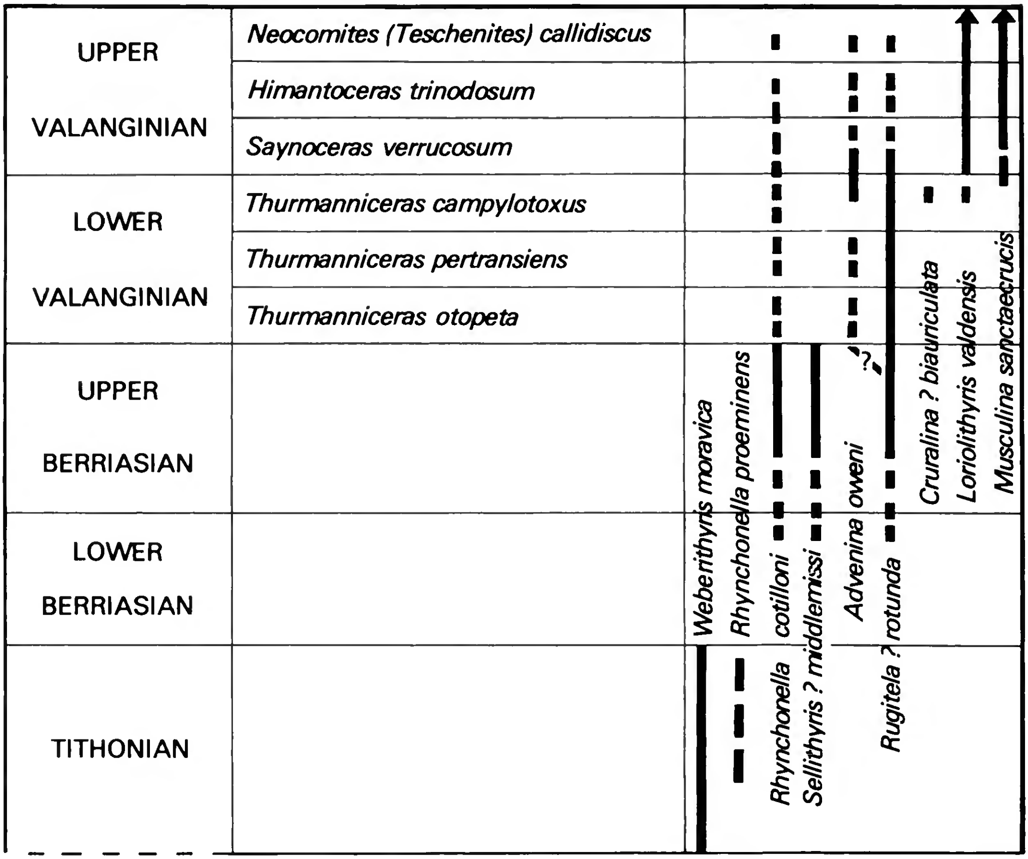


Fig. 21 Stratigraphical ranges of brachiopods from Provence and beyond, referred to in this paper.

species and those of the Lower Cretaceous of Provence. This supports Ager, Childs & Pearson's suggestion (1972: 224) that in post-Kimmeridgian times *R.* s.s. diversified into shallower-water habitats.

Sellithyris is first represented in the Berriasian by *S. carteroniana* (d'Orbigny) in the southern French Jura (p. 179). *S.*? *middlemissi* sp. nov. is at present known only from the Berriasian of Provence. The association of species of *Rugitela* with clay-bearing sediments has already been noted (Owen 1973: 128). *Rugitela*? *rotunda* sp. nov. from the Berriasian is associated with micritic limestones in Provence. This small species may represent a sub-Tethyan diversification of the genus and possibly a paedogenetic offshoot from *Rugitela* s.s. *R.*? *rotunda* possesses secondary callus thickening in the pedicle umbo, a feature which has not been observed in *Advenina oweni* sp. nov. The former species also has more strongly developed dental lamellae and a more acute septalium. The two species differ by external and internal details but *R.*? *rotunda* does not appear to be far removed from *Advenina* gen. nov., both lacking a median ridge in the septalium.

Sellithyris? *middlemissi*, *Rhynchonella cotilloni* and *Rugitela*? *rotunda* are stratigraphically distinctive, occurring in the Berriasian, the latter two species ranging into the Upper Valanginian (Fig. 21), whilst *Advenina oweni* is recorded from the late Lower Valanginian of Provence and ranges into the Upper Valanginian.

The brachiopod fauna described from the Berriasian–Lower Valanginian of Provence suggests that a number of new species are associated with the Lower Cretaceous marine transgressions, and may indicate a 'speciation event'.

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Charixa Lang and *Spinicharixa* gen. nov., cheilostome bryozoans from the Lower Cretaceous

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Synopsis

Seven species of non-ovicellate anascans with pluriserial to loosely multiserial colonies are described from the Barremian–Albian of Europe and Africa. The genus *Charixa* Lang is revised and the following species assigned: *C. vennensis* Lang from the U. Albian Cowstones of Dorset, *C. lhuydi* (Pitt) from the U. Aptian Faringdon Sponge Gravel of Oxfordshire, *C. cryptocauda* sp. nov. from the Albian Mzinene Fm. of Zululand, *C. lindiensis* sp. nov. from the Aptian of Tanzania, and *C.*? sp. from the Barremian Makatini Fm. of Zululand. *Spinicharixa* gen. nov. is introduced for *Charixa*-like species with multiple spine bases. Two species are described: *S. pitti* sp. nov., the type species, probably from the Urgoniana Fm. (?Aptian) of Spain, and *S. dimorpha* from the M.–U. Albian Gault Clay of Kent. All previous records of L. Cretaceous cheilostomes are reviewed. Although attaining a wide geographical distribution, cheilostomes remained uncommon, morphologically conservative and of low species diversity until late Albian–early Cenomanian times.

Introduction

An outstanding event in the fossil history of the Bryozoa is the appearance, radiation and dominance achieved by the Cheilostomata during the latter part of the Mesozoic. Aspects of this event have been discussed by several authors (e.g. Cheetham & Cook *in* Boardman *et al.* 1983; Larwood 1979; Larwood & Taylor 1981; Schopf 1977; Taylor 1981*a*; Voigt 1981). Comparative morphology provides strong evidence for regarding living cheilostomes as the sister group of living ctenostome bryozoans (Cheetham & Cook *in* Boardman *et al.* 1983). Fossil ctenostomes have been found as borings (e.g. Pohowsky 1978) and bioimmured casts (e.g. Voigt 1980 and references therein) antedating the oldest cheilostomes, and it is generally thought that a soft-bodied bryozoan resembling the living ctenostome *Arachnidium* was the ancestor of the Cheilostomata (Banta 1975; cf. Dzik 1975 for an alternative view of cheilostome origins). Primitive cheilostomes differ from ctenostomes of the *Arachnidium* type principally in having a hinged operculum to close the orifice, and rigid calcification in parts of the zooid body wall.

Although cheilostomes first appear in the terminal Portlandian Stage of the Jurassic, their major diversification was delayed until the late Cretaceous; rapid morphological evolution and cladogenesis commenced in the late Albian or early Cenomanian and culminated in cheilostome dominance of fossil bryozoan faunas by about the Campanian or Maastrichtian. This spectacular diversification has tended to overshadow the considerable period of slow cheilostome evolution during the 50 million years or so of early Cretaceous time. Little attention has been paid to this 'quiet' phase of cheilostome evolution.

Relatively few species of cheilostomes are known from the L. Cretaceous (see below, p. 198). The principal aim of this paper is to describe a group of species which are especially typical of the L. Cretaceous. They have loosely organized pluriserial or multiserial colonies, and lack ovicells and avicularia. A review of these and other early cheilostomes provides a base from which to assess the later diversification of the group.

Abbreviations of specimen repositories are: British Museum (Natural History)—BMNH; Université Claude Bernard, Lyon—UCBL; South African Museum—SAM; Muséum National

Bull. Br. Mus. nat. Hist. (Geol.) **40** (4): 197–222

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d'Histoire Naturelle, Paris—MNHN. All photographic figures are scanning electron micrographs, using back-scattered electrons, of uncoated specimens, except Figs 25–27 which are of coated latex casts.

Review of Lower Cretaceous cheilostomes

Of the few cheilostomes recorded from the L. Cretaceous, the majority are of late Albian age and most are European or North American occurrences. The literature of L. Cretaceous cheilostomes is reviewed below, chronologically by date of publication.

Mantell (1844) was the first author to describe a probable cheilostome from the L. Cretaceous. *Crisia johnstoniana* Mantell appears to be an encrusting, uniserial cheilostome with caudate zooecia. It was later assigned to *Rhammatopora* Lang by Lang (1915), a genus here regarded as a junior synonym of *Herpetopora* Lang. Mantell's original description gives the geological horizon of *C. johnstoniana* as the Shanklin Sand, while a later description (Mantell 1854) specifies the horizon and locality as the Greensand of Maidstone, presumably Aptian Lower Greensand (Lang 1915). Unfortunately the whereabouts of Mantell's material is unknown and the exact nature of the species is difficult to assess from his stylized illustrations.

In 1853 d'Orbigny described two species of '*Membranipora*' from the French L. Cretaceous. *M. neocomensis* [sic], from the Neocomian of Saint-Sauveur, Yonne, is merely mentioned without description or figure. Voigt (1968) regarded the species as a *nomen nudum*. The poorly-preserved type specimen (d'Orbigny Collection, MNHN No. 5205) is a multiserial colony possibly related to *Wawalia* Dzik. *M. constricta*, from the Aptian of Les Croutes, Yonne, has been restudied by Voigt (1968), who assigned the species to '*Membranipora*' s.l. but noted the lack of correspondence between the putative type specimen (d'Orbigny Collection, MNHN No. 5691) and d'Orbigny's figures (d'Orbigny 1853: pl. 728, figs 9–10). The putative type specimen (see Voigt 1968: pl. 7, fig. 8) and a second specimen in the d'Orbigny Collection have been examined. Both are poorly-preserved multiserial cheilostomes with zooecia that have broad, striated cryptocysts, resembling *Wawalia crenulata* Dzik (see opposite) but without a significant proximal gymnocyst.

Vine (1890*a*, *b*) described 5 cheilostome species from the Red Chalk of Hunstanton, most of which is Middle and Upper Albian though some may be Cenomanian (H. G. Owen, personal communication 1985). One of Vine's Red Chalk species was new, *Membranipora gaultina*, and the others were determined as *Membranipora fragilis* (d'Orbigny), *M. elliptica* (?) (Hagenow), *M. obliqua* (?) (d'Orbigny) and *Hippothoa simplex* (d'Orbigny). *M. gaultina* Vine is a uniserial species with strongly caudate zooecia which was later made the type of *Rhammatopora* by original designation by Lang (1915). Thomas & Larwood (1960) characterized *Rhammatopora* by the presence of numerous apertural spine bases, but scanning electron microscope study of the type specimen (BMNH D2062) of *M. gaultina* has failed to confirm these structures and *Rhammatopora* is here regarded as a synonym of *Herpetopora* Lang. The specimen (BMNH D2052) from Hunstanton described by Vine (1890*a*, *b*) as *Hippothoa simplex* (d'Orbigny) is undoubtedly conspecific with *Herpetopora gaultina* (Vine) (see Thomas & Larwood 1960: 384). *Membranipora fragilis* (d'Orbigny), *sensu* Vine is represented by an abraded specimen (BMNH D2053) of an encrusting multiserial cheilostome which is too poorly preserved for identification. The single specimen (BMNH D2054) determined as *Membranipora elliptica* (?) (Hagenow) by Vine is another encrusting multiserial cheilostome distinguished by the presence of numerous small polymorphs (probably kenozooecia) which surround and separate the autozooecia. Worn ovicells appear to be present. The whereabouts of Vine's specimen of *Membranipora obliqua* (?) (d'Orbigny) is not known. Vine (1890*a*) described the specimen as being a dichotomously branched colony with oval, thick-walled zooecia.

Later, in 1892, Vine recorded '*Membranipora gaultina* Vine' and '*Hippothoa*?' (presumably also *Herpetopora gaultina*) from the Gault (Albian) of Barnwell, Cambridge, together with a specimen described as '*Membranipora fragilis* d'Orbigny variety?' from the Gault of Folkestone. The description of this latter species resembles *Spinicharixa dimorpha* sp. nov. (see below, p. 214) except for the apparent presence of ovicells.

Lang (1915) divided Vine's material of *Membranipora gaultina* into two species, *Rhammatopora gaultina* (Vine) for specimens from the Gault Clay, and *R. vinei* Lang for specimens from the Red Chalk in which the mural rim is slightly straighter. The doubtful significance of such a minor feature led Thomas & Larwood (1960) to synonymize the two species. In the same paper Lang described *Charixa vennensis*, a new species belonging to a new monotypic genus, from the Albian Cowstones of Charmouth, Dorset. This species is revised below (p. 201).

Etheridge (1901) described *Lunulites abnormalis* from the L. Cretaceous of Queensland, and in 1902 described *Membranipora*? *wilsonensis* from the L. Cretaceous of New South Wales, Australia. Both species are in need of redescription and are difficult to assess from Etheridge's original descriptions and figures. *L. abnormalis* forms low cone-shaped colonies with well-defined rows of rectangular zooecia. Although colonies appear to be lunulitiform, assignment of the species to the genus *Lunulites* is questionable; *Lunulites* is unknown in pre-Coniacian deposits. *M.*? *wilsonensis* has multiserial encrusting colonies with rhombic zooecia. An unusual feature is the presence of a 'spot' (?spine base) on each of the transverse zooecial walls.

Wilbertopora mutabilis from the Albian Fort Worth Formation of Texas was the first L. Cretaceous cheilostome to be described from N. America (Cheetham 1954). The species has since been recorded (Cheetham 1975) from various other formations within the Albian–Cenomanian Washita Group of Texas. *W. mutabilis* is an encrusting anascan with a multiserial arrangement of zooecia, although some colonies have the first few generations of zooecia arranged uniserially. Qualitative and quantitative characters are highly variable. Some colonies, including topotypes, have ovicells, but ovicells are apparently absent in certain 'populations'. Avicularia or avicularian-like polymorphs may be present or absent, and variously shaped. Small orificial spine bases are sometimes present and, more rarely, lateral spine bases.

An additional cheilostome from the Fort Worth Formation was described by Thomas & Larwood (1956) as *Pyripora texana.* This is a predominantly uniserial species in which the pyriform zooecia have relatively broad caudae. Pairs of tiny apertural spines have been described by Cheetham (1975) in some zooecia of putative conspecific colonies which Cheetham records from several formations in the Washita Group.

A possible junior synomym of *Wilbertopora mutabilis* is *Membranipora*? *kiowana* described by Scott (1970) from the Kiowa Formation of Kansas, a formation of similar age to those in Texas containing *W. mutabilis* (Cheetham 1975: 552). Dzik (1975), however, refers *M.*? *kiowana* to his new genus *Wawalia.*

Masse & Walter (1974) briefly describe and figure an un-named fossil from the U. Barremian of Orgon in southern France which they identify tentatively as a cheilostome. The cheilostome affinities of this 'membranipore' are extremely doubtful; the 'zooecia' seem too small (0·16–0·18 mm long) and their arrangement too orderly for an early cheilostome bryozoan.

Larwood's (1975) review of pre-Cenomanian cheilostomes includes mention of three specimens of un-named species from the British Albian which await full description. One of these (BMNH D7477), from the U. Greensand of Warminster, resembles *Wilbertopora mutabilis.* A second (BMNH D31158), from the Haldon Hills, is too poorly preserved for description, while a third (BMNH D38164), from the Cowstones near Charmouth, is described as a unilamellar membranimorph. Larwood also mentions a pyriporid cheilostome from the Aptian of Alexander Island, Antarctica, which was described by B. J. Taylor in an unpublished paper presented to the 2nd International Conference of the International Bryozoology Association in Durham during 1971.

Wawalia crenulata was described by Dzik (1975) from the U. Valanginian and L. Hauterivian of Wawal in central Poland. This unusual multiserial species, the second oldest known cheilostome, is characterized by the thickly calcified vertical walls of the zooecia, regular interserial linkage between zooecia *via* communication pores, a wide cryptocyst which is striated, and irregular pores in the proximal gymnocyst. Specimens of *W. crenulata*, or a closely related species, also occur in the Hauterivian of Lincolnshire and Yorkshire.

The late Aptian Faringdon Sponge Gravel of Faringdon in Oxfordshire is renowned for its rich fauna of cyclostome bryozoans (Canu & Bassler 1926) to which Pitt (1976) added the first record of a cheilostome, '*Membranipora*' *lhuydi.* This species is redescribed below (p. 203) and

assigned to *Charixa*. The introductory remarks in Pitt's paper note the existence of a single specimen of a Neocomian cheilostome from South Africa, as yet undescribed.

Finally, *Pyriporopsis portlandensis* Pohowsky, described originally from the Portlandian Stage of the Jurassic (Pohowsky 1973; Taylor 1981*b*), has now been recorded (Ensom 1985) from the Scallop Member of the Purbeck Limestone Formation in Dorset. This extends the range of the species into the Berriasian Stage of the Cretaceous.

Systematic descriptions

Order **CHEILOSTOMATA** Busk, 1852

Suborder **ANASCA** Levinsen, 1909

Family **ELECTRIDAE** Stach, 1937

Non-brooding anascans (and inferred non-brooding anascans) constitute a primitive, paraphyletic group of cheilostomes. Recent representatives of this group are usually divided between the families Electridae and Membraniporidae (e.g. Ryland & Hayward 1977). The former family comprises genera in which the gymnocyst is relatively well developed (e.g. *Electra*, *Pyripora*), the latter those in which it is absent or greatly reduced (e.g. *Membranipora*, *Conopeum*). All the pre-Cenomanian anascans described here have moderately to well developed gymnocysts and are consequently assigned to the Electridae. This is likely to be the more primitive of the two living families. The Membraniporidae are regarded as secondarily reduced (Silén 1942).

Dzik (1975) introduced the Family Wawalidae for *Wawalia* Dzik, *Pyriporopsis* Pohowsky, *Charixa* Lang, *Pyripora* d'Orbigny, *Fissuricella* Voigt and possibly *Rhammatopora* Lang. He distinguished the family from the Electridae by the absence of spines. However, occasional zooecia have spines in some colonies of *Pyripora texana* Thomas & Larwood (see Cheetham 1975) and *Charixa lindiensis* sp. nov. (p. 205). This variability raises doubts about the wisdom of using presence or absence of spines as a distinguishing character at this taxonomic level. *Charixa* Lang and *Spinicharixa* gen. nov. are here placed in the Electridae rather than the Wawalidae.

Genus *CHARIXA* Lang, 1915

TYPE SPECIES. *Charixa vennensis* Lang 1915, by original designation.

REVISED DIAGNOSIS. Colonies encrusting, pluriserial with irregularly-arranged, partly contiguous zooecia; distolateral buds usually orientated at a narrow angle to the parent zooecium. Autozooecia ovoidal to pyriform in outline shape; proximal gymnocyst moderately to well developed, sometimes forming a cauda; cryptocyst narrow, steeply sloping, pustulose; spine bases absent or limited to a small distal pair; pore chambers present or presumed to be present. Kenozooecia may occur. Ovicells and avicularia absent.

REMARKS. Based on a revision of the type species, *Charixa* is here used to include primitive, *Electra*-like anascans in which colonies are pluriserial and irregular, the cryptocyst is narrow, steeply sloping, pustulose and has a crenulate margin with the surrounding gymnocyst, and spine bases are absent or limited to a sporadically-developed distal (oral) pair. Colony form resembles *Pyriporopsis* Pohowsky but the zooecia of *Charixa* do not have the radially striated cryptocysts and very thick vertical walls typical of *Pyriporopsis*. The tendency of *Charixa* colonies to form pluriserial clumps of irregularly arranged zooecia distinguishes the genus from *Pyripora* d'Orbigny, in which the colony is typically uniserial or occasionally narrowly multiserial and the zooecia are more regularly caudate. However, it should be emphasized that generic concepts in these primitive anascans are made difficult by the paucity of available morphological characters and high levels of phenotypic plasticity among species.

In his original description of *Charixa*, Lang (1915) remarked on the beaded 'termen' (i.e. the opesial margin). As in *Rhammatopora*, Thomas & Larwood (1956) interpreted these beads as

spine bases. However, scanning electron microscope study has failed to reveal the presence of spine bases in Lang's type material, and it is likely that the beads observed by Lang were pustules of the cryptocyst or corrosion pits.

RANGE. Aptian (?Barremian)–Albian. It is unclear whether the genus ranges out of the Lower Cretaceous. A species described as *Pyripora magna* by Larwood (1973), from Campanian (*mucronata* Zone) Chalk of Norfolk, is possibly assignable to *Charixa*.

Charixa vennensis Lang 1915
Figs 1–3

1915 *Charixa vennensis* Lang: 501; pl. XVII, figs 5–6.

HOLOTYPE. BMNH D22950. Cowstones, Upper Greensand, Upper Albian (*inflatum* Zone, *varicosum* Subzone). Black Ven, Charmouth, Dorset, England.

PARATYPES. A large suite of specimens was apparently used by Lang when describing *C. vennensis*, and these are labelled as paratypes in the BMNH collections. They consist of the following: D20483 (2 specimens)–D20487 'Albian, zone of *Hoplites interruptus*, Gault, Bed 3, Section d, Black Ven, Charmouth'; D22931–41, D22946–49, D22951–85 'Albian, zone of *Mortoniceras rostratum*, Cowstones, Black Ven, Charmouth'; D23021–24 'Albian, Gault, zone of *Hysteroceras varicosum*, Dunton Green, N. of Sevenoaks, Kent, F. Möckler Colln'. Of these paratypes, only D22948–49 and D22951–52 can be positively determined as *C. vennensis*. The remainder are too heavily corroded for identification, reveal only the featureless underside of the colony, or belong to different species (the Dunton Green specimens are *Herpetopora gaultina* (Vine) and *Spinicharixa dimorpha* sp. nov.).

DESCRIPTION. Colonies are encrusting, uniserial or more typically pluriserial with the zooecia arranged in irregular fans and clusters (Figs 1a, 2). Budding is distal and distolateral, the latter usually at a small angle (<60°) to the parent zooecium but occasionally at right angles. Depending on the exact angle of distolateral budding, distolaterally budded zooecia may be separated from or partly contiguous with distally budded ones arising from the same parent zooecium.

Autozooecia are generally pyriform and have well-developed proximal gymnocysts forming caudae less than half the total length of the zooecium. However, in crowded areas the proximal

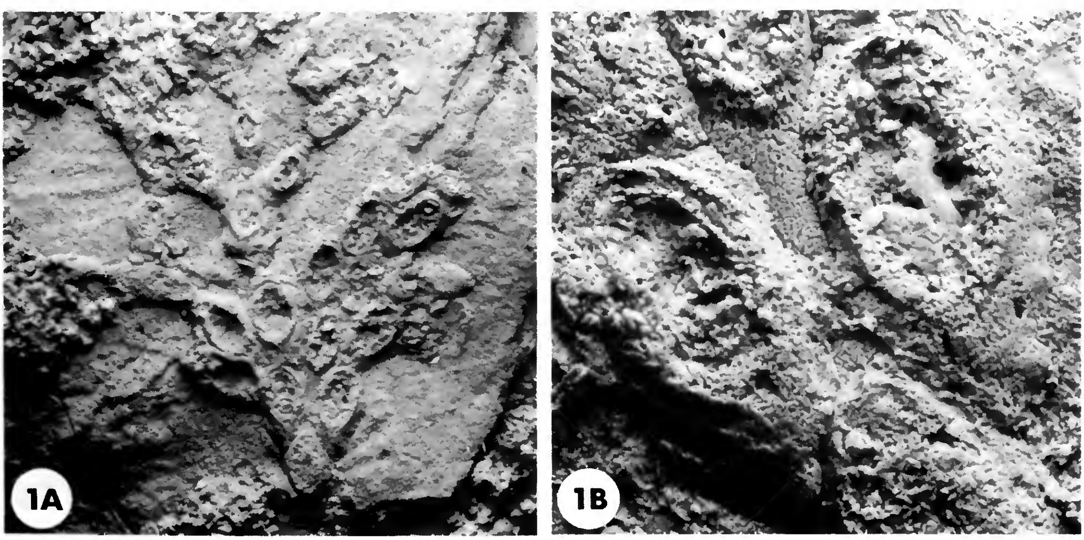


Fig. 1 *Charixa vennensis* Lang. BMNH D22950. Holotype. Cowstones (Albian); Black Ven, Dorset. 1A, fan-like colony-form, × 28; 1B, poorly-preserved zooecia with pustulose cryptocysts, × 140.

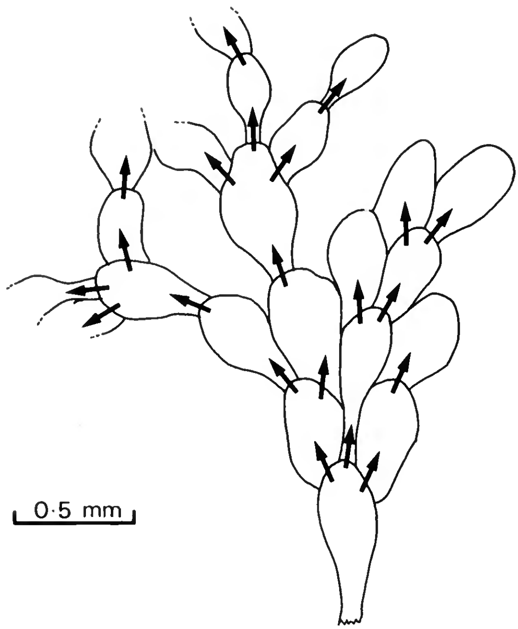


Fig. 2 *Charixa vennensis* Lang. BMNH D22950. Holotype. Outline diagram of zooecia to show budding pattern. Arrows indicate directions of budding. Note the abnormally small zooecia budded at the distal ends of the branches on the left.

gymnocyst is reduced and the autozooecium is more elliptical in shape. Autozooecial size varies considerably within colonies (Fig. 1a; Table 1, p. 219), length averaging 0·51 mm and width 0·24 mm in the holotype. The occurrence of small autozooecia budded from distinctly larger autozooecia in the holotype (Figs 1a, 3a) led Lang (1915) to suggest rejuvenescence of growth. Opesiae are oval, and almost twice as long ($\bar{x} = 0{\cdot}24$ mm) as wide ($\bar{x} = 0{\cdot}14$ mm). The cryptocyst is steeply sloping, pustulose, and has a crenulate margin with the surrounding gymnocyst (Fig. 1b). There are no indications of spine bases (cf. Thomas & Larwood 1956). Some autozooecia have regenerations and others are occluded by closure plates which are flat or slightly depressed, and bear crescent-shaped depressions made by the opercular sclerites (Fig. 3b). Pore chambers are not visible in the holotype nor in those paratype specimens which are unequivo-

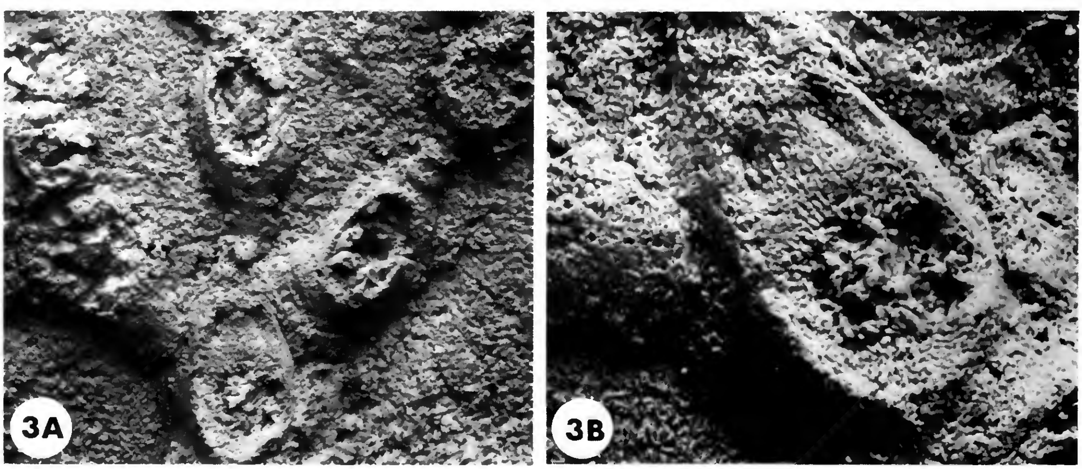


Fig. 3 *Charixa vennensis* Lang. BMNH D22950. Holotype. Cowstones (Albian); Black Ven, Dorset. 3A, autozooecium with closure plate budding small autozooecia distally and distolaterally, × 90; 3B, damaged closure plate with an opercular impression, × 230.

cally conspecific with it, but they can be seen in possibly conspecific colonies in which only the undersides of the zooecia are visible.

Kenozooecia may occur filling irregular spaces between autozooecia. They are polygonal in outline and have slightly concave edges. The frontal surface seems to be completely calcified, i.e. opesiae are lacking.

The ancestrula has not been observed. Avicularia and ovicells are unknown.

REMARKS. Unfortunately, none of the available specimens of *C. vennensis* is well preserved. Adherent sand grains obscure zooecial details and on removal leave pits in the calcification. These corrosion pits, emphasized by staining with watercolour paint, were possibly misinterpreted as spine bases by Thomas & Larwood (1956).

Colonies encrust fragments of mollusc (probably bivalve) shells.

DISTRIBUTION. U. Albian (*inflatum* Zone, *varicosum* Subzone), known only from Black Ven, Charmouth.

Lang (1915) records *C. vennensis* from two stratigraphical levels on Black Ven. These he gives as Bed 3 in the *Hoplites interruptus* Zone, and the Cowstones in the lower part of the *Mortoniceras rostratum* Zone. The former horizon is probably the clayey silt regarded as M. Albian *dentatus* Zone by Wilson *et al.* (1958: 141). However, none of the specimens from this level are sufficiently well preserved to be confirmed as *C. vennensis*. Lang's second horizon probably corresponds with the 'Lower Sands with Cowstones' of Wilson *et al.* (1958) and is of the U. Albian *inflatum* Zone, *varicosum* Subzone (H. G. Owen, personal communication 1985).

Charixa lhuydi (Pitt 1976)
Figs 4–5

1976 '*Membranipora*' *lhuydi* Pitt: 65; pl. 1, figs A–D.

HOLOTYPE. BMNH D52494. Faringdon Sponge Gravel, U. Aptian (*nutfieldensis* Zone). Little Coxwell Pit, Faringdon, Oxfordshire. L. J. Pitt Colln.

PARATYPE. BMNH D52495. Same details as holotype.

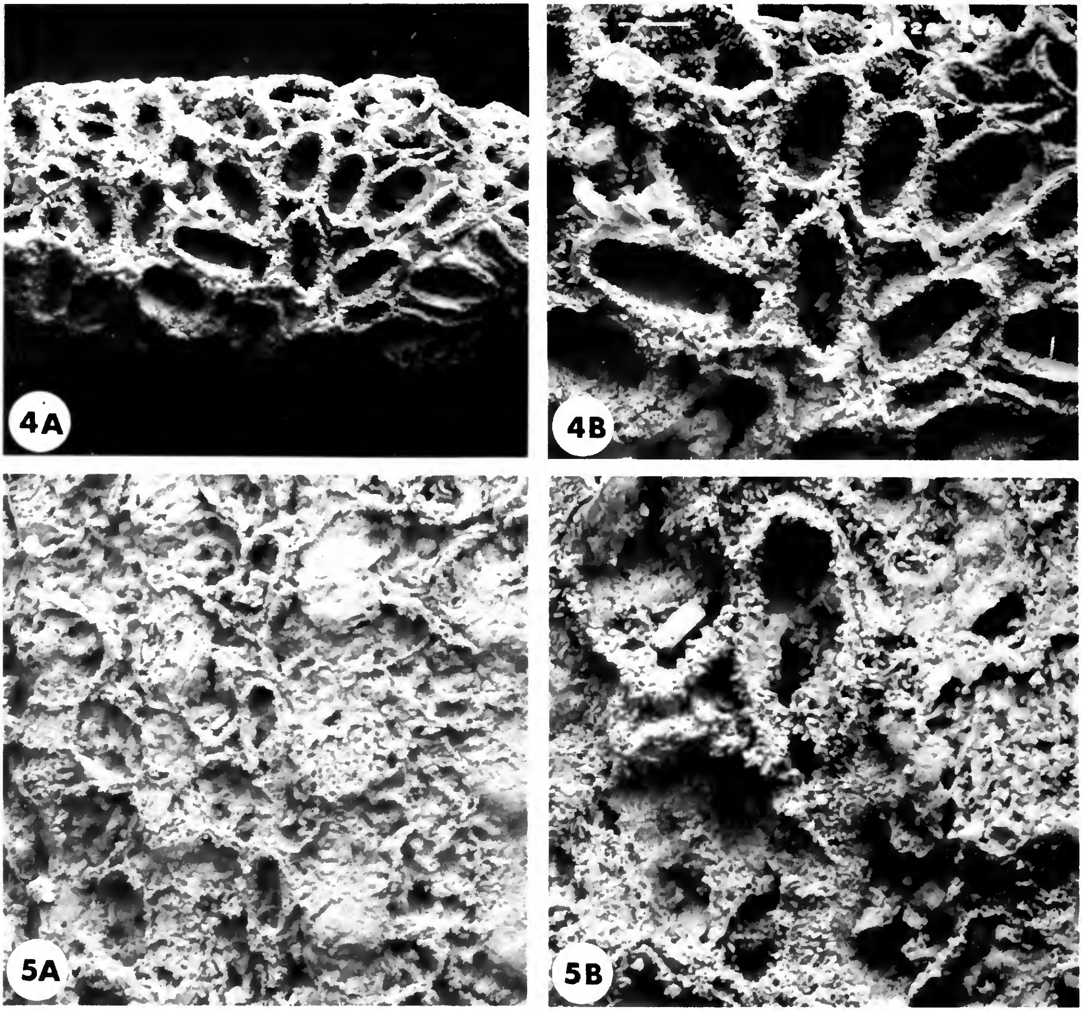
ADDITIONAL MATERIAL. BMNH D54190–200, Faringdon Sponge Gravel, locality unknown, G. J. Hinde Colln. BMNH D55067, as holotype, A. G. Davis Colln. BMNH D55068, as holotype, G. F. Elliott Colln.

DESCRIPTION. Colonies are encrusting and comprise irregular pluriserial patches of zooecia (Fig. 4a) which sometimes show multilamellar overgrowth. Zooecial orientations and budding positions are difficult to ascertain in the poorly-preserved material which is available. However, in one specimen (BMNH D54191) a line of caudate autozooecia appears to bud distolateral non-caudate autozooecia of the type more typical for the species (Fig. 5).

Autozooecia are usually elliptical in outline (Fig. 4b) and have a slight proximal gymnocyst. Rarely, autozooecia are pyriform (Fig. 5b) and have a caudate proximal gymnocyst about half the length of the zooecium. In the holotype, autozooecial length averages 0·44 mm and width 0·33 mm. Opesiae are elongate elliptical and occupy most of the frontal surface of the majority of autozooecia. Cryptocysts are usually obscured by calcite cement but appear to be steeply sloping and seem to be pustulose. Unequivocal closures and regenerations have not been observed. Communication pores are present as windows in vertical walls (see Pitt 1976: pl. 1, fig. D), but the expected presence of pore chambers has not been confirmed in this poorly-preserved material.

Some of the irregular spaces between autozooecia appear to be occupied by kenozooecia with extensive opesiae. These were perhaps misidentified as broken ovicells by Pitt (1976). Avicularia and unequivocal ovicells are absent. The ancestrula is unknown.

REMARKS. Since Pitt's (1976) original description of this species several additional specimens have become available. Unfortunately these share the poor preservation of the holotype and paratype. A considerable growth of calcite cement obscures surface details, and several of the



Figs 4–5 *Charixa lhuydi* (Pitt). Faringdon Sponge Gravel (Aptian). Fig. 4, BMNH D55068, Little Coxwell Pit, Faringdon; 4A, colony encrusting a branch fragment of *Meliceritites*, × 37; 4B, autozooecia with oval opesia, × 65. Fig. 5, BMNH D54191, locality unknown; 5A, line of three caudate autozooecia (centre) growing in the furrow of an echinoid spine, × 37; 5B, caudate autozooecium, × 112.

colonies are abraded. However, the finding of a colony (BMNH D54191) with a line of caudate autozooecia (Fig. 5) suggests assignment of the species to *Charixa*. These caudate autozooecia follow a furrow in the echinoid spine encrusted by the colony. Their distolateral buds appear to be non-caudate autozooecia of the kind which predominate in *C. lhuydi* colonies. By comparison with *Spinicharixa dimorpha* (p. 214), it is thought that the caudate autozooecia represent an initial runner-like growth across the substratum.

All known specimens except one encrust spines of regular echinoids. Colonies often occupy the entire circumference of the spine and are usually absent from the collar region. Spines of Recent echinoids are frequently fouled by epizoans (including bryozoans) while the echinoid is still alive (Mortensen 1928: 27), but remain free of encrusters on the collars of the spines where muscles attaching the spine to its base are situated. It appears possible that *C. lhuydi* was a life

associate of echinoids, although the single colony (BMNH D55068) of *C. lhuydi* encrusting an erect branch of the cyclostome *Meliceritites* shows that the association was not entirely obligatory for the bryozoan.

Distribution. U. Aptian (*nutfieldensis* Zone), Faringdon Sponge Gravel of Faringdon, Oxfordshire, England.

Charixa cryptocauda sp. nov.
Figs 6–7

Holotype. SAM PCZ7306. Mzinene Formation, Albian, subdivision IV or V of Kennedy & Klinger (1975). Stream bed and bank exposures in eastern limb of broad meander, ENE of sisal factory, north of Hluhluwe, Zululand, South Africa. Locality 51 of Kennedy & Klinger (1975). W. J. Kennedy Colln.

Paratype. SAM PCZ7307. Same details as holotype.

Name. In reference to the cauda becoming hidden by later zooecial buds.

Description. Colonies are encrusting with uniserial chains of zooecia (Fig. 6a) or pluriserial sheets of irregularly-arranged zooecia (Fig. 7a). Initial budding appears to have been predominantly distal, giving uniserial chains, but later distolateral and occasionally proximolateral budding produced zooecia which infilled the substrate between the uniserial chains and overgrew the caudae of earlier zooecia.

Autozooecia are elliptical to pyriform in outline shape, depending upon the length of the proximal gymnocyst which can be short or can form a distinct cauda up to half the total length of the zooecium. Average autozooecial length in the holotype is 0·53 mm, width 0·24 mm. Opesiae are usually about twice as long as wide, and roughly elliptical but with a tendency to be square-ended. The cryptocyst is narrow, steeply sloping, pustulose, and has a crenulate border with the surrounding gymnocyst. Many zooecia have large distolateral and proximolateral communication pores visible as windows in the vertical walls. Distal pore chambers may be well-developed (Fig. 7b). Regenerations occur rarely and closure plates are seldom found. However, an autozooecium in the paratype has a closure plate which is slightly depressed below the level of the mural rim, flat-surfaced, and incompletely calcified leaving an elongate median perforation (Fig. 6b). The closure plate bears a semicircular impression of the operculum which was evidently about 0·10 mm wide.

Kenozooecia occur abundantly in the holotype (Fig. 7c). They are irregular, mainly triangular or diamond-shaped, and have slightly concave sides. Kenozooecial cryptocysts resemble those of autozooecia but the opesiae are smaller and less regular. Bud fusion appears to occur in the formation of at least some of the kenozooecia (Fig. 7d).

Ovicells and avicularia have not been observed. The ancestrula is unknown.

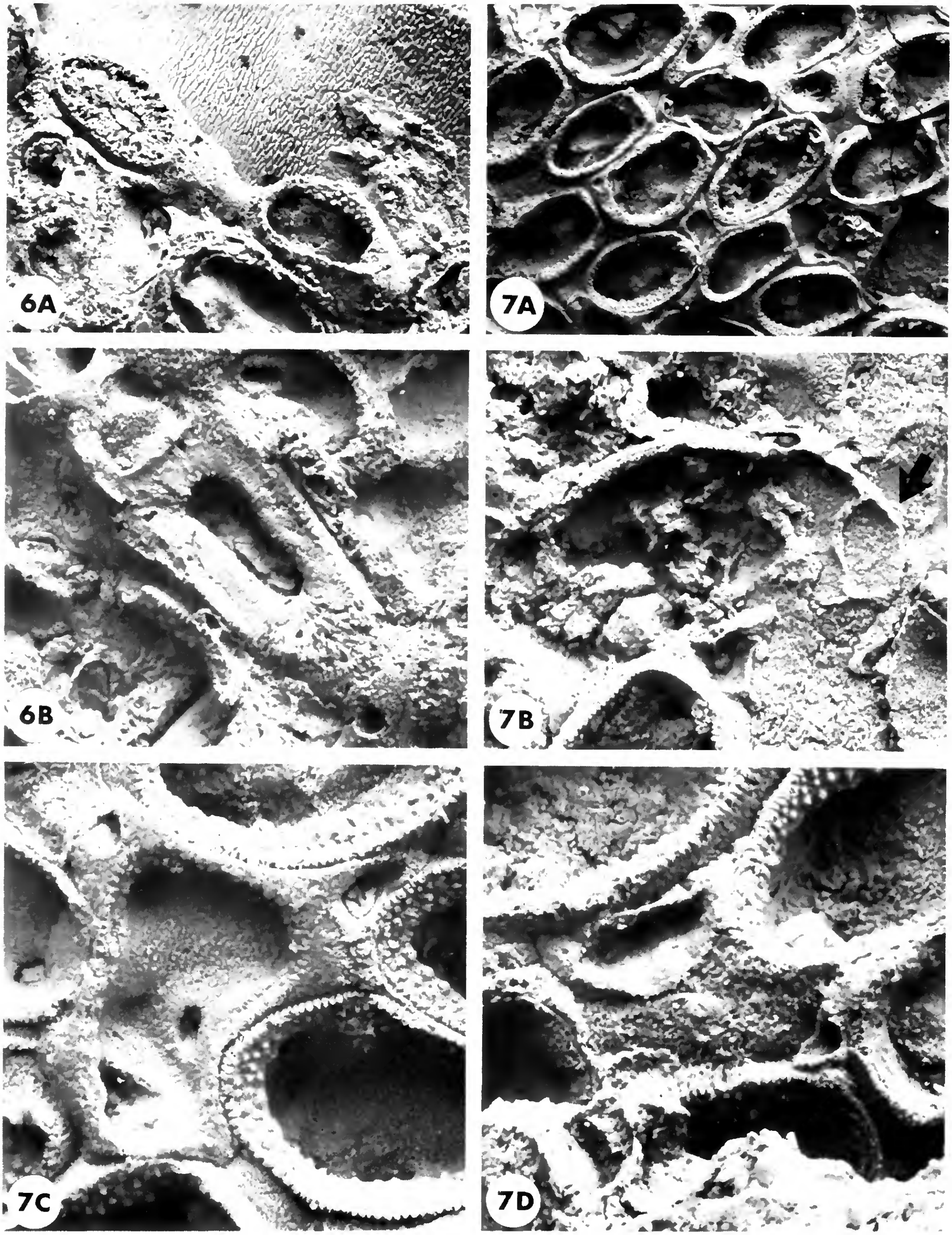
Discussion. *C. cryptocauda* is distinguished from previously described species of *Charixa* and similar genera by the unusual overgrowth of the caudae of early budded autozooecia by later autozooecia, particularly kenozooecia. The result is reminiscent of the Recent hiantoporid anascan *Dactylostega prima* Hayward & Cook, 1983 in which autozooidal boundaries become obscured by the budding of interzooidal avicularia and ?kenozooids onto the colony surface.

The holotype colony encrusts the epifaunal gastropod *Eriptycha* sp., whereas the paratype colony encrusts an oyster together with serpulids and foraminifers.

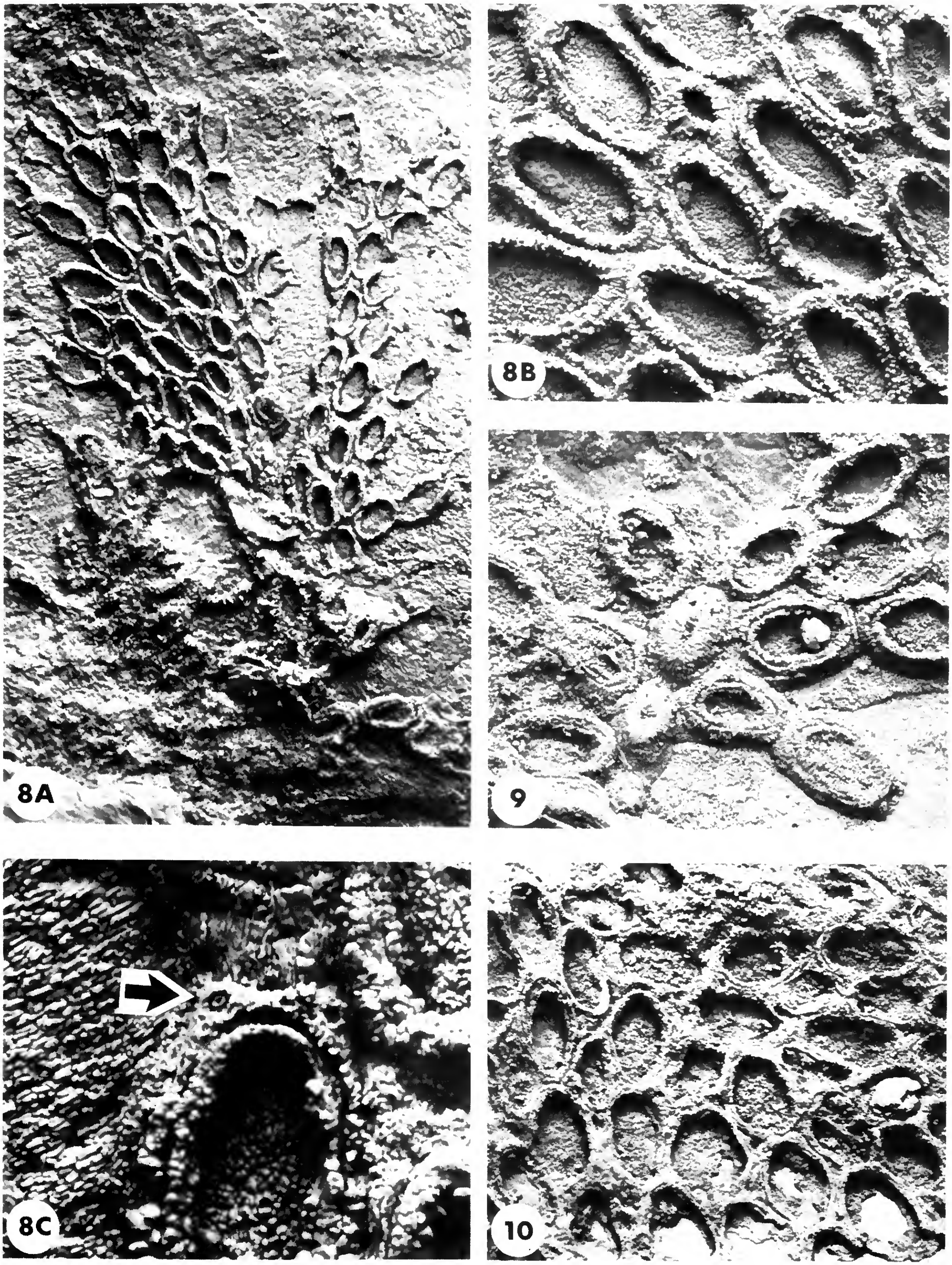
Distribution. Albian (subdivision IV or V of Kennedy & Klinger, 1975), Mzinene Fm., of Hluhluwe, Zululand, South Africa.

Charixa lindiensis sp. nov.
Figs 8–10

Holotype. BMNH D55025a. Aptian. 1–1·5 miles from Utimbe on the Libobe road, Lindi, Mtwara Province, Tanzania. G. M. Stockley Colln.



Figs 6–7 *Charixa cryptocauda* sp. nov. Mzinene Formation (Albian); N. of Hluhluwe, Zululand. Fig. 6, SAM-PCZ 7307, paratype; 6A, caudate autozooecia, × 93; 6B, perforated closure plate of autozooecium with opercular scar, × 130. Fig. 7, SAM-PCZ 7306, **holotype**; 7A, crowded autozooecia and kenozooecia, × 53; 7B, abraded autozooecium showing large distal pore chamber (arrow), × 150; 7C, kenozooecium filling the area between autozooecial opesia, × 200; 7D, incipient kenozooecium arising as two or three separate buds onto the proximal gymnocyst of an autozooecium, × 190.



Figs 8–10 *Charixa lindiensis* sp. nov. Aptian; Lindi, Mtwara Province, Tanzania. Fig. 8, BMNH D55025a, **holotype**; 8A, lobate colony-form, × 24; 8B, autozooecia and a diamond-shaped kenozooecium, × 83; 8C, pair of distal spine bases (arrow), × 240. Fig. 9, BMNH D55026b, paratype, astogenetically early autozooecia with closure plates and regeneration rims, × 67. Fig. 10, BMNH D55026a, paratype, oblique view of crowded, worn autozooecia, × 46.

PARATYPES. BMNH D55025b, encrusting the same substrate as the holotype. BMNH D55026a, b, Aptian, Utimbe, Lindi, Mtwara Province, Tanzania. G. M. Stockley Colln.

NAME. From the Tanzanian district of Lindi.

DESCRIPTION. Colonies are encrusting and pluriserial with zooecia sometimes arranged in fan-like expansions (Fig. 8a) or irregular clumps (Fig. 10), although early zooecia may have a looser, more uniserial configuration (Fig. 9).

Autozooecia are elliptical to slightly pyriform in shape (Figs 8b, 9). The proximal gymnocyst is of slight to moderate length, not exceeding one quarter of total zooecial length. Autozooecia are relatively small, averaging 0·41 mm long by 0·20 mm wide in the holotype (Table 1, p. 219). Opesiae are elongate ellipsoidal, about twice as long as wide, sometimes slightly square-ended. Rarely autozooecia have a pair of distal spine bases (Fig. 8c). These are small, oval, and have a concentric inner ring (as in *Spinicharixa* spp. and *Callopora lineata*). A steeply sloping cryptocyst appears to be present but details are obscured by surface growth of cement crystals. Pore chambers have not been observed. Several autozooecia have a single, rarely two, regenerations. Closure plates occur in a few early autozooecia of specimen D55026b (Fig. 9). They are convex and weathered to reveal a radiating microstructure and a narrow uncalcified median area. A pair of slit-like opercular sclerite impressions on the closure plate indicates an operculum width of about 0·04 mm.

The holotype has a kenozooecium (Fig. 8b) which is elongate diamond-shaped with a broad gymnocyst surrounding the opesia. Avicularia and ovicells are absent. The ancestrula has not been observed.

REMARKS. *C. lindiensis* is distinguished from other species of *Charixa* by the consistently small size of the zooecia, and the very occasional development of a pair of distal spine bases. In the sporadic occurrence of distal spine bases *C. lindiensis* resembles the uniserial Albian species *Pyripora texana* (see Cheetham 1975), although it is not clear whether the spine bases in *P. texana* also have a concentric ring structure.

Each colony encrusts either the exterior or the interior surface of an oyster.

DISTRIBUTION. Aptian of Utimbe, Lindi Province, Tanzania.

Colonies of *C. lindiensis* were found among a sample of oysters in the mollusc collections of the BMNH. These oysters were collected from the area of Utimbe in about 1930 by G. M. Stockley, then employed by the Geological Survey of Tanganyika and later to become Director. The Utimbe area is mapped only as undiffentiated Cretaceous (1 : 500,000 scale map produced by BP Shell Petroleum Development Co., Tanganyika, and dated 1960), and the oysters themselves are not age diagnostic (N. J. Morris, personal communication 1985). However, the correspondence files of the BMNH contain a letter dated 23 June 1930 from L. R. Cox to G. M. Stockley concerning the Utimbe specimens. The letter notes the existence of associated fragments of the Aptian ammonite *Cheloniceras* which were determined by L. F. Spath.

Charixa? sp.
Fig. 11

MATERIAL. BMNH D55062. Bed 18, Makatini Fm., Barremian. Locality 170 of Kennedy & Klinger (1975), 2 km NW of the store on north side of stream, Mlambongwenya Spruit, Northern Zululand, South Africa. W. J. Kennedy Colln.

DESCRIPTION. An encrusting colony which is partly uniserial but mainly pluriserial with zooecia arranged irregularly. Distolateral buds are usually orientated at a small angle to the axis of the parental zooecium.

Autozooecia are large, averaging about 0·72 mm long by 0·34 mm wide, and elliptical to pyriform in shape with variable development of the proximal gymnocyst (Fig. 11a). Opesia are elliptical and generally twice as long as wide. No cryptocyst is visible; radial fissures in the mural rim seem to represent the weathered microstructural fabric of the gymnocyst (Fig. 11a–b). Some autozooecia have closure plates (Fig. 11b) but opercular scars are not evident.

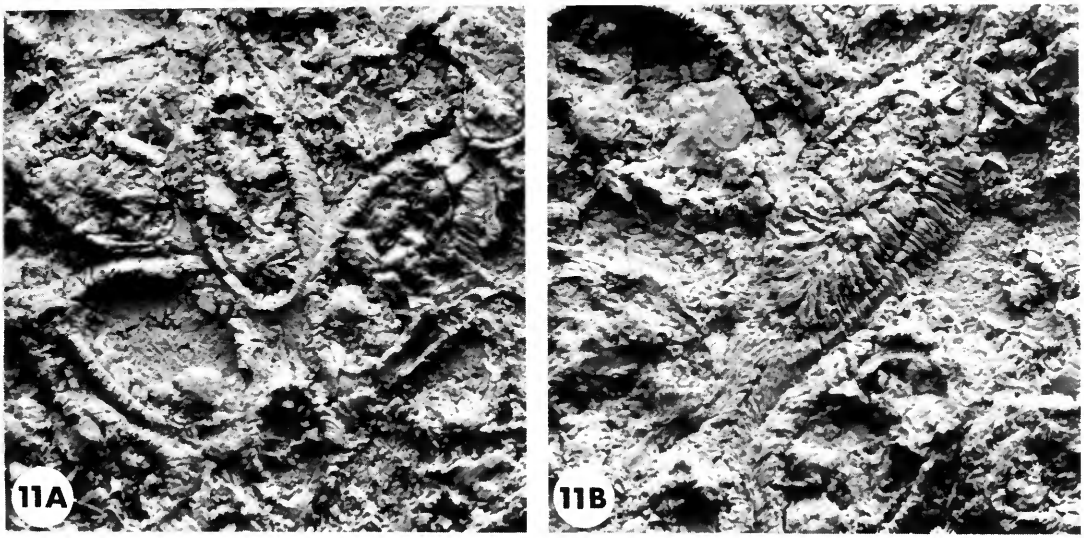


Fig. 11 *Charixa*? sp. BMNH D55062, Makatini Formation (Barremian); Mlambongwenya Spruit, Zululand; 11A, worn autozooecia with open opesia, × 64; 11B, worn autozooecium with closure plate, × 73.

A few irregular, space-filling kenozooecia with wide opesiae occur. Ovicells and avicularia have not been observed.

Remarks. Colony-form and zooecial shape in this Barremian species are typical of *Charixa* but a cryptocyst is apparently lacking. Therefore assignment to *Charixa* is questionable. Full description of the species must await the availability of more material.

Genus *SPINICHARIXA* gen. nov.

Type species. *Spinicharixa pitti* sp. nov.

Diagnosis. Colonies encrusting, pluriserial or multiserial with quite regularly arranged zooecia. Autozooecia ovoidal to pyriform in outline shape; proximal gymnocyst slightly to well developed, sometimes forming a cauda; cryptocyst narrow, steeply sloping, pustulose; spine bases numerous, each with an inner concentric ring, indenting the margin of the cryptocyst; pore chambers present in ontogenetically young zooecia but apparently resorbed in many older zooecia. Ancestrula budding a distal zooecium and possibly additional zooecia proximally and laterally. Kenozooecia may occur. Ovicells and avicularia absent.

Name. Like *Charixa* but spinose.

Remarks. *Spinicharixa* is introduced for primitive, non-ovicellate anascans resembling *Charixa* but possessing numerous spine bases ringing the opesiae of the autozooecia. Zooecial arrangement tends to be more regular in *Spinicharixa* than *Charixa.* In *S. pitti* interzooecial gaps, common in species of *Charixa*, are seldom found, and parts of the essentially multiserial colonies have a regular quincuncial arrangement of subrhomboidal zooecia. *S. dimorpha*, however, is more *Charixa*-like in having an essentially pluriserial colony-form with some interzooecial gaps.

Range. ?Aptian–Albian.

Spinicharixa pitti sp. nov.
Figs 12–18

Holotype. UCBL EM30401b. Probably Urgoniana Formation, ?Aptian. Utrillas, Spain, Coquand Colln 1867.

Paratypes. UCBL EM30401a, c, d, e, colonies encrusting same substrate as holotype. EM30402, details as for holotype. EM30409 (several groups of zooecia which may represent many colonies or a single fragmented colony), details as for holotype but Verneuil Colln.

Name. For Leslie J. Pitt, in recognition of his many years of research on Aptian bryozoans.

Description. Colonies are encrusting, with the first 4 or 5 generations of zooecia arranged uniserially (Fig. 14) before rapidly expanding into a multiserial sheet. Multiserial parts of colonies have a compact, near quincuncial arrangement of zooecia (Fig. 12) with little interzooecial space. However, linear series of more caudate zooecia (Fig. 13a) may sometimes be distinguished within the multiserial sheet suggesting that growth pattern may perhaps have resembled that of *S. dimorpha* which is described below (p. 215). Well-preserved growing edges have not been observed.

Autozooecia are elliptical to rounded rhomboidal in shape, averaging 0·41 mm long by 0·25 mm wide. Opesiae are extensive and elliptical in shape, sometimes slightly square-ended. The proximal gymnocyst is usually short but is fairly well developed in a few lineal series of zooecia. The cryptocyst is moderately broad, steeply sloping and pustulose (Fig. 15c) with a crenulate margin with the surrounding gymnocyst. Pustules are arranged in 4 or 5 ill-defined alternating rows, become sparser basally, and are lacking from the distal end of the zooecium. Each autozooecium has 4–7 spine bases, generally paired, which are situated within the gymnocyst but indent the cryptocyst (Fig. 17). The spine bases (Fig. 18) are circular or elliptical (elongated parallel to the edge of the opesia) and variable in diameter ($\bar{x} = 0{\cdot}02$ mm; observed range = 0·01–0·04 mm). The edge of the spine base is slightly raised and an inner concentric ring is situated within the conical central depression. Large pore chambers may occur in distal and distolateral positions. Several autozooecia, possibly all occluded by closure plates, have

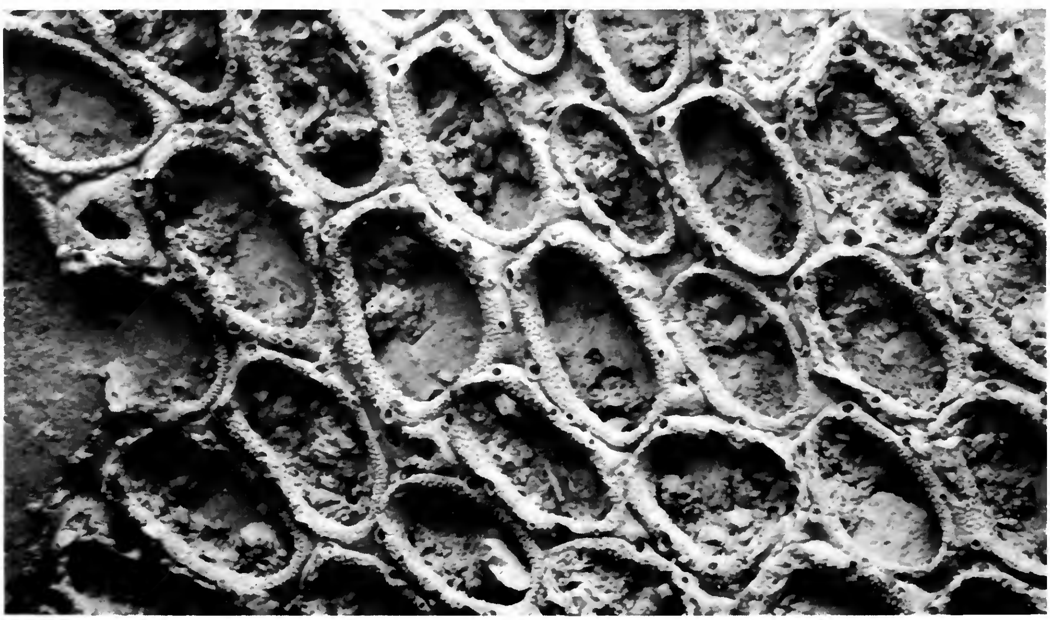
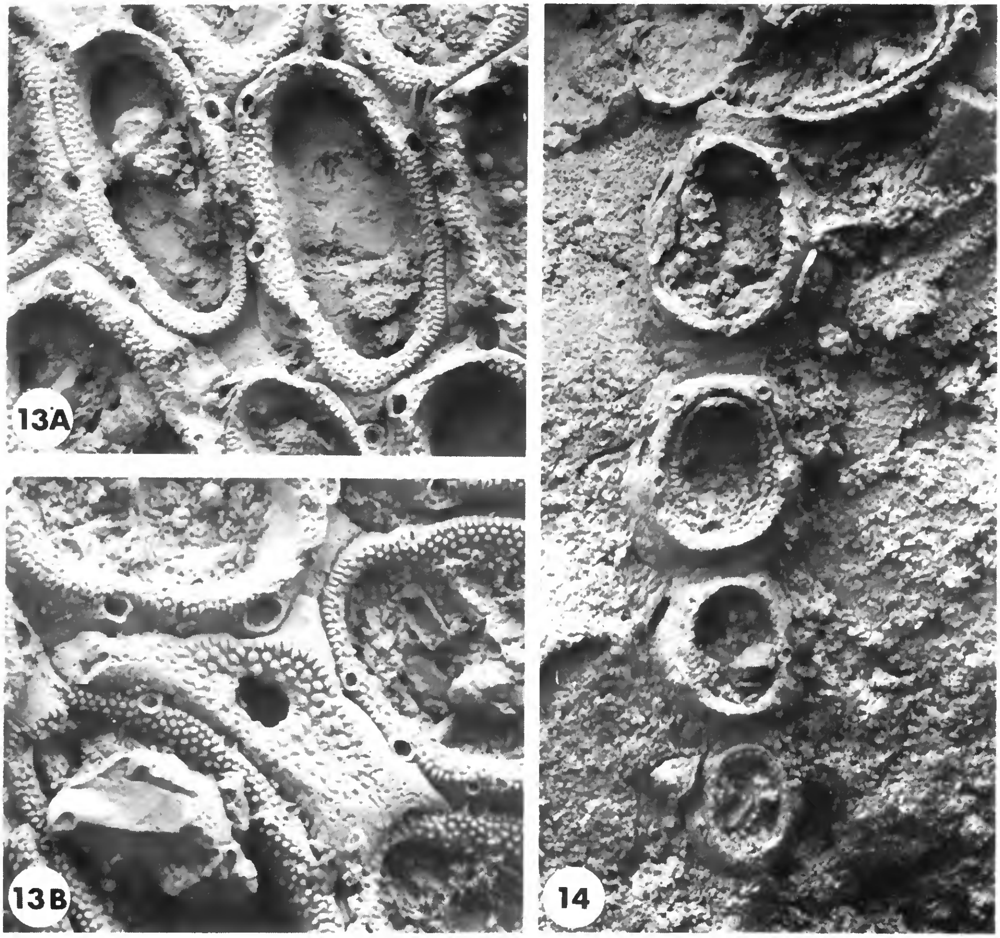


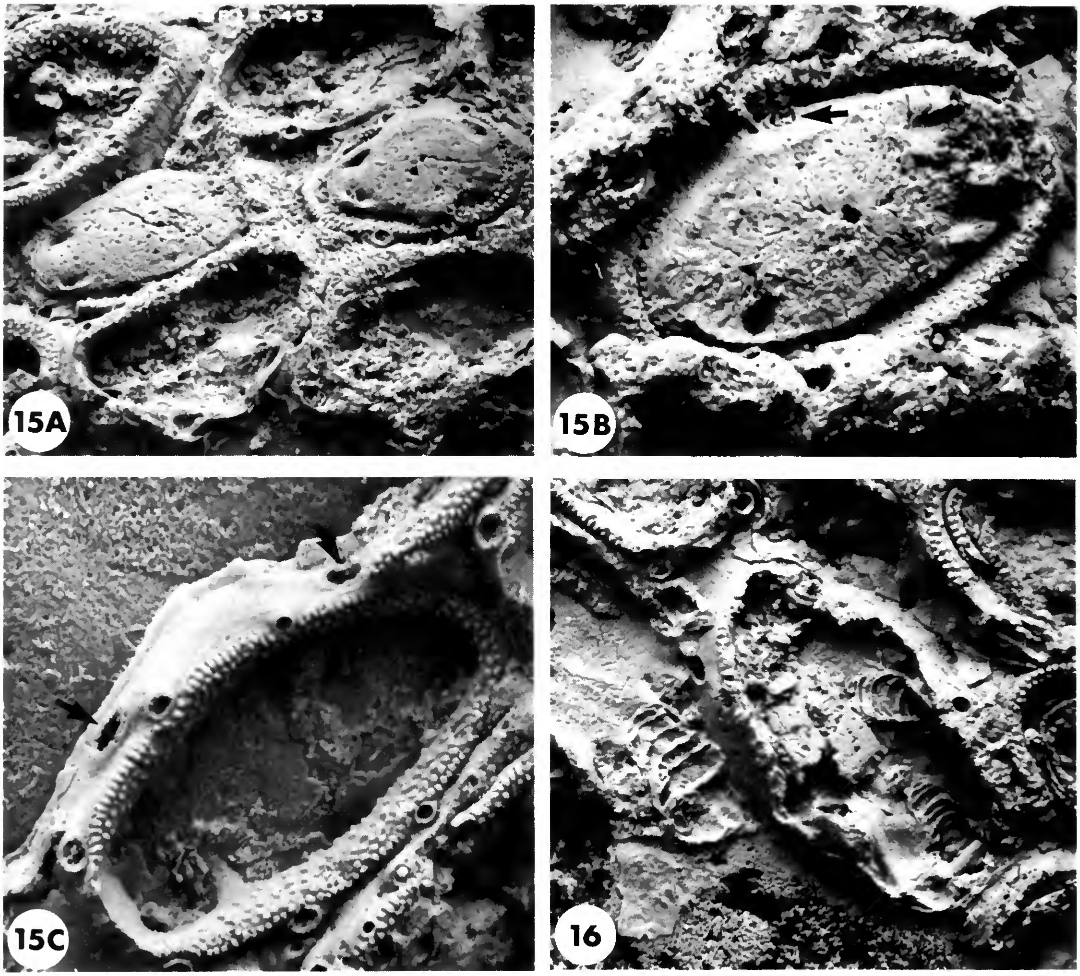
Fig. 12 *Spinicharixa pitti* gen. et sp. nov. UCBL EM30401b, **holotype**; probably Urgoniana Formation (?Aptian); Utrillas, Spain; slightly oblique view of colony surface, × 65.



Figs 13–14 *Spinicharixa pitti* gen. et sp. nov.; probably Urgoniana Formation (?Aptian); Utrillas, Spain. Fig. 13, UCBL EM30401b, **holotype**; 13A, autozooecia showing spine bases and pustulose cryptocysts, × 110; 13B, kenozooecium, × 134. Fig. 14, UCBL EM30401d, paratype; ancestrula and first three generations of budded autozooecia arranged uniserially, × 143.

unusual elongated pore chambers which are partitioned transversely by up to 10 arcuate walls convex towards the interior of the zooecium (Fig. 16). Communication pore windows in free exterior walls are large and elliptical. Interserial communication between zooecia is suggested by the presence in some zooecia of proximolateral pores as well as distal and distolateral pores (Fig. 15c). Regeneration rims may occur (Fig. 14). Closure plates are of two types: in one the plate is convex and joins the crenulate edge of the gymnocyst; in the second the plate is surrounded by a deep marginal furrow and has a sloping edge (sometimes penetrated by spine bases located inwards of the usual spine bases) and a flat top (Fig. 15a, b). The first type is interpreted as a simple closure, whereas the second may be a closure plate formed by a zooid with a regeneration. Closure plates of the latter type may have a system of irregular radial surface fissures, and an opercular scar with sclerite impressions 0·07–0·08 mm apart.

The ancestrula and early buds (Fig. 14) are well preserved in paratype colony UCBL EM30401d but less well preserved in the holotype colony. The ancestrula is small, elliptical in shape, and broad in comparison with later zooids, about 0·16 mm long by 0·14 mm wide. Swellings of the gymnocyst, partly obscured by sediment, may represent one or a pair of spine



Figs 15–16 *Spinicharixa pitti* gen. et sp. nov.; probably Urgoniana Formation (?Aptian); Utrillas, Spain. Fig. 15, UCBL EM30401b, **holotype**; 15A, two autozooecia with closure plates, × 90; 15B, autozooecium with closure plate incorporating a spine base (arrow), × 224; 15C, autozooecium with windows (arrows) of pore chambers in free exterior wall, × 148. Fig. 16, UCBL EM30402, paratype, broken pore chambers partitioned by arcuate plates, × 120.

bases situated about mid-length. There is a single distally-budded periancestrular autozooecium with 4 spine bases. The first 4 or 5 generations of zooecia are arranged uniserially and show a progressive increase in size.

Kenozooecia (Figs 13b, 17) occur as space-filling structures which are smaller than autozooecia, and generally have 4 concave sides. The cryptocyst is broad, flat, has coarse pustules and a crenulate margin with the gymnocyst. Opesiae are small and elliptical.

Ovicells and avicularia are not present.

Remarks. *Spinicharixa pitti* is distinguished from previously described non-ovicellate anascans by the abundant spine bases with a distinctive concentric structure, and from *S. dimorpha* by the lack of dimorphism of autozooecia.

There is a slight resemblance between *S. pitti* and *Distelopora bipilata* described by Lang (1915) from the Chalk Marl of Cambridge. In this Cenomanian species, however, the spine bases appear not to have an inner ring, and the cryptocyst seems to overlap the gymnocyst. All

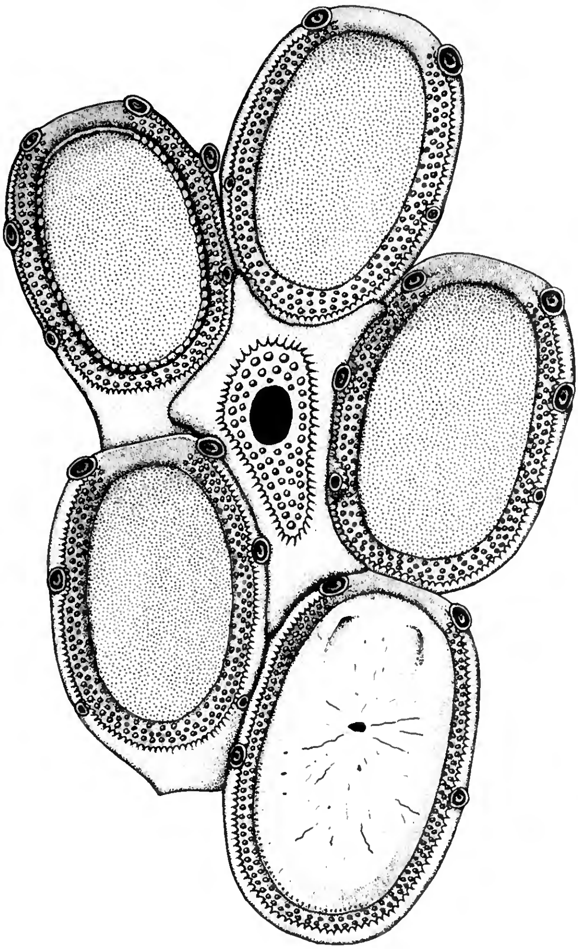


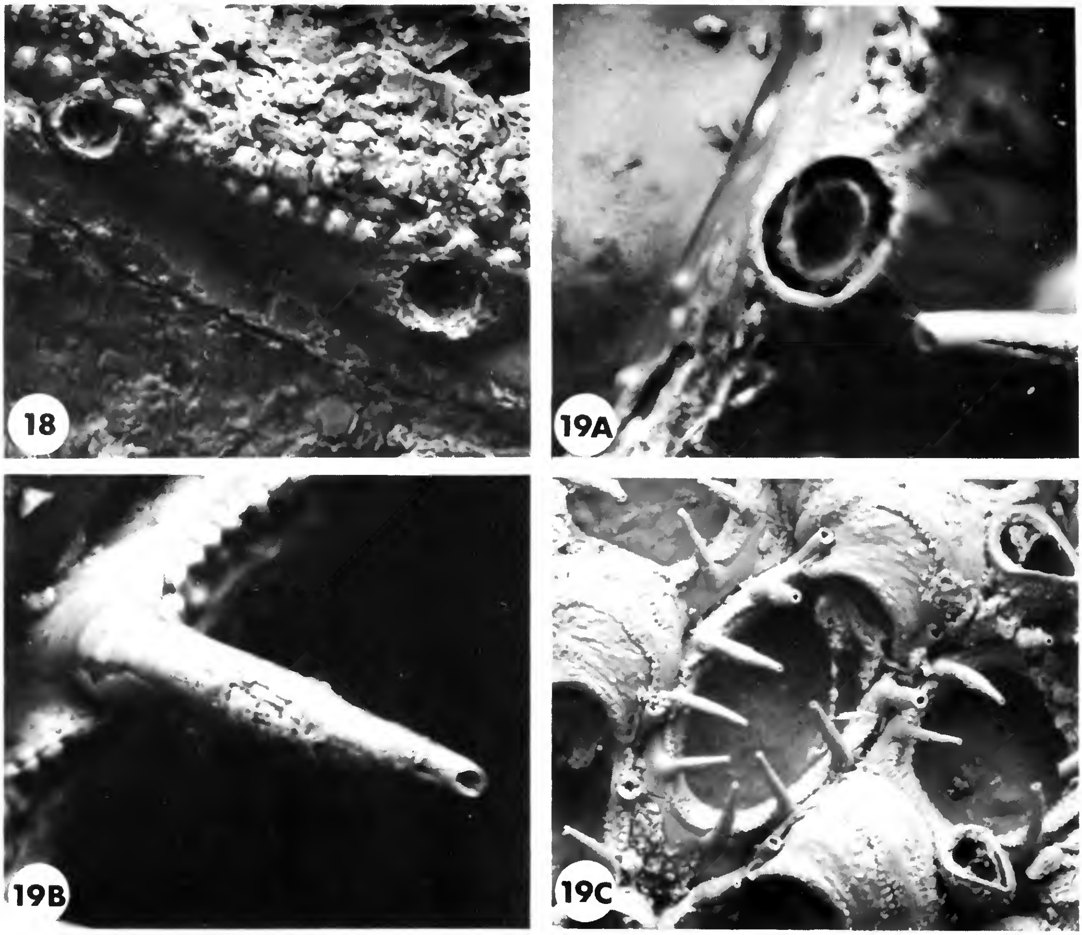
Fig. 17 *Spinicharixa pitti* gen. et sp. nov. Composite drawing of 5 autozooecia surrounding a kenozooecium. The autozooecium bottom right has a closure plate of the type formed after regeneration; the autozooecium top left has a regeneration rim.

specimens of *D. bipilata* consist of small colonies and it is possible that ovicells and avicularia developed during later stages of colony growth.

The spine bases of *S. pitti* strongly resemble those of the living *Callopora lineata*. In both species the spine base has a crater-like shape with an inner concentric ring (Figs 18, 19a). The intact spines of *C. lineata* are hollow and pointed, and overarch the frontal membrane of the zooid (Figs 19b, c). A similar morphology is envisaged for *S. pitti*, although the high variability in spine base diameter could indicate more variation in spine size than in *C. lineata*. The basal area of the spine seems to represent a point of weakness from which the spines may have become detached accidentally or perhaps shed during the ontogeny of the zooid.

Colonies of *S. pitti* encrust the epifaunal gastropod *Paraglauconia lujani* (de Verneuil & Collomb). Most occur on apical whorls but colony UCBL EM30409f is situated on the inner lip, an area which would have been covered by mantle tissue during the life of the gastropod, implying that the gastropod became encrusted *post mortem*.

Distribution. ?Aptian. There are uncertainties about the exact stratigraphical level from which these museum specimens were collected. A Barremian–Cenomanian sequence exposed in the region of Utrillas has been described by Aguilar *et al.* (1971). Cassiopid gastropods like those encrusted by *S. pitti* appear to be present in the Urgoniana Formation which is partly Barremian but mostly Aptian. The same gastropod species also occurs in the L. Aptian (*forbesi* Zone) Punfield Marine Bed of Dorset (Cleevely *et al.* 1984).



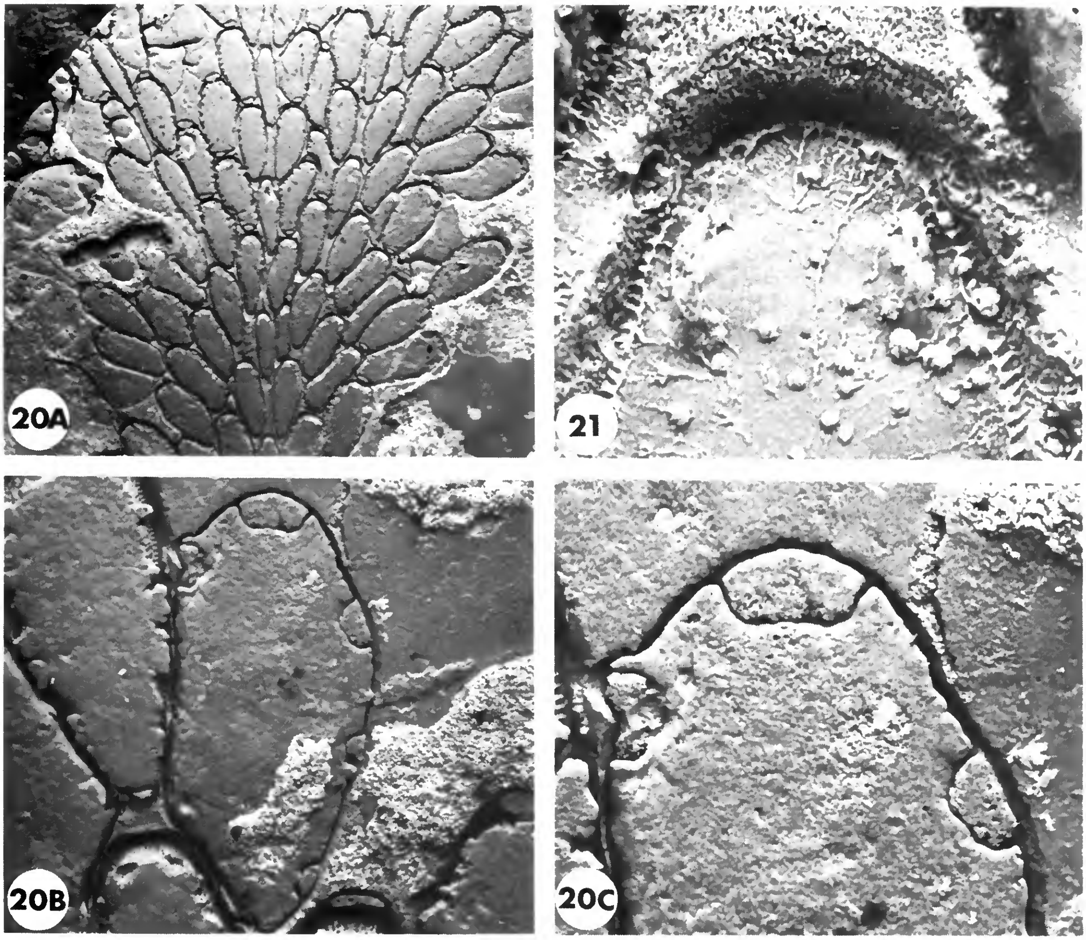
Figs 18–19 Spines and spine bases in *Spinicharixa* and *Callopora*. Fig. 18, *Spinicharixa pitti* gen. et sp. nov.; UCBL EM30402, paratype; probably Urgoniana Formation; Utrillas, Spain; two spine bases with inner concentric rings, × 530. Fig. 19, *Callopora lineata* (Linné), BMNH Zoology Department 1911.10.1.513a; Recent; Durham Coast; 19A, spine base with inner concentric ring, × 740; 19B, intact spine, × 610; 19C, ovicelled autozooecium with spines over-arching the opesiae, × 125.

Spinicharixa dimorpha sp. nov.
Figs 20–27

?1892 *Membranipora fragilis* d'Orbigny var?; Vine: 155.

Holotype. BMNH D53152a. Cristatum Nodule Bed, U. Gault Clay, U. Albian (*inflatum* Zone, *cristatum* Subzone). Naccolt Brickworks, Wye, Ashford, Kent. A. Gale Colln. Preserved as a mould on the surface of a phosphatic steinkern.

Paratypes. BMNH D53152b, c, on the same substrate as the holotype. D35361, Gault Clay, Dunton Green, Sevenoaks, Kent, D. Forbes Colln (probably from the M.–U. Albian *lautus* Zone nodule bed; H. G. Owen personal communication, 1984). D46898, Gault Clay Bed 9, U. Albian (*inflatum* Zone, *orbignyi* Subzone), Greatness Lane, Sevenoaks, Kent, J. S. H. Collins Colln. These four specimens are, like the holotype, preserved as moulds on the surface of phosphatic steinkerns. D55066 (several broken colonies), L. Gault Clay, M. Albian (*loricatus* Zone, *intermedius* Subzone), Copt Point, Folkestone, Kent, A. Gale & D. Horne Colln.



Figs 20–21 *Spinicharixa dimorpha* gen. et sp. nov.; Gault Clay (Albian); phosphatic moulds of colony undersides. Fig. 20, BMNH D53152a, **holotype**; Naccolt Brickworks, Ashford, Kent; 20A, caudate and non-caudate autozooecia, × 14; 20B, newly-budded non-caudate autozooecium with well-defined pore chambers, × 65; 20C, same autozooecium showing large distal and smaller distolateral pore chambers, × 137. Fig. 21, BMNH D35361, paratype; Dunton Green, Sevenoaks, Kent; distal part of the closure plate of a caudate autozooecium showing lunate impressions of the opercular sclerites, × 330.

NAME. In reference to the two types of autozooecia.

DESCRIPTION. Colonies are encrusting and pluriserial (Fig. 20a). The budding pattern is very distinctive (Fig. 22); lines of long, narrow, caudate autozooecia bud distolateral autozooecia which are short, broad and non-caudate and are orientated subparallel to their parent autozooecium. These non-caudate autozooecia bud further non-caudate autozooecia distally and distolaterally to infill the space between the lineal series of caudate autozooecia. Irregular interzooecial gaps are often left and the autozooecia are less tightly packed than in *S. pitti*. Non-caudate autozooecia occasionally give rise to new lineal series of caudate zooecia, originating as distal buds and generally separated from earlier series of caudate autozooecia by two generations of non-caudate autozooecia.

Autozooecia are large, caudate autozooecia averaging 1·35 mm long by 0·26 mm wide and having a pyriform outline, whereas non-caudate autozooecia average 0·92 mm long by 0·36 mm

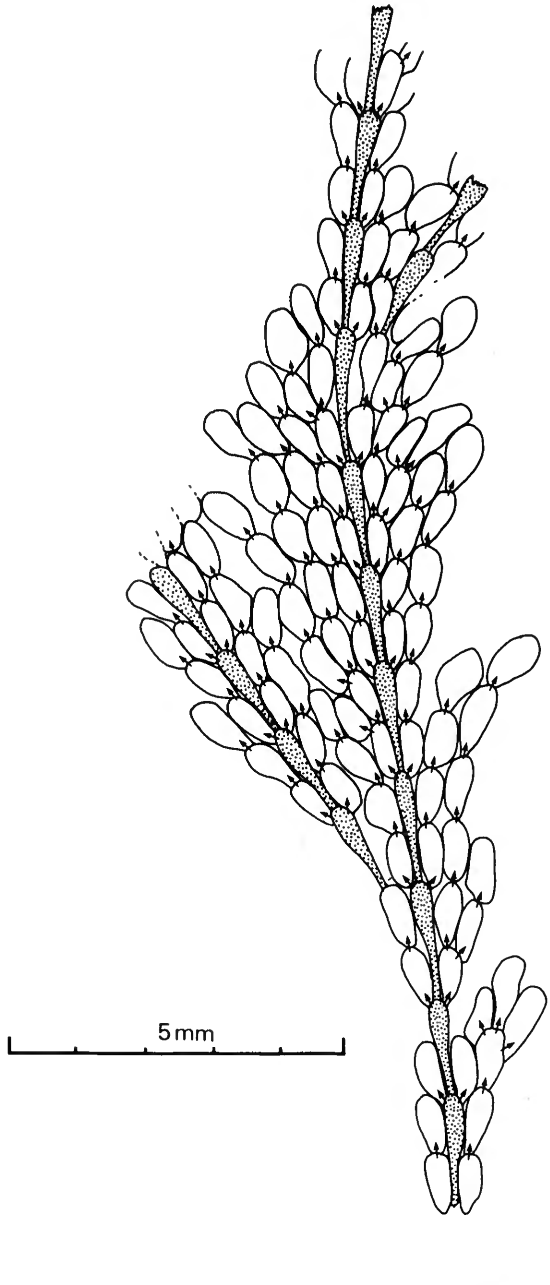


Fig. 22 *Spinicharixa dimorpha* gen. et sp. nov. Outline diagram of paratype BMNH D35361 to show budding pattern. Caudate autozooecia are stippled; arrows indicate budding directions.

wide and are subelliptical in outline. Opesiae are extensive in both types of autozooecia. Gymnocysts are narrow except in caudate zooecia in which the proximal gymnocyst is elongate. Cryptocysts are also narrow and are steeply sloping, pustulose, and have crenulate boundaries with the gymnocysts. Small, circular to elliptical spine bases occur in variable numbers (Fig. 25b). Caudate autozooecia may have up to eight pairs of spine bases, but non-caudate autozooecia, especially those distant from caudate series, have fewer, apparently sometimes restricted to a distal pair. The spine bases are often located within the gymnocystal furrows between the opesiae of adjacent autozooecia (Fig. 25a). In contrast to *S. pitti*, they rarely indent the outer edge of the cryptocyst. However, like *S. pitti*, well-preserved spine bases have an inner concentric ring resembling that found in the Recent anascan *Callopora lineata*.

Pore chambers are conspicuous only in newly budded autozooecia, in which a large distal pore chamber occurs together with up to three pairs of smaller pore chambers situated disto-laterally, laterally or proximolaterally (Fig. 20b, c). Ontogenetically older autozooecia proximal of the growing edge appear to lose their pore chambers. Ontogenetic series of the large distal pore chambers seem to show a progressive resorption of the distal exterior wall of the pore chamber occurring concurrently with thickening of the proximal interior wall (Figs 23, 24). This eliminates the pore chamber in older zooecia and sometimes appears to sever continuity between zooecia *via* communication pores. However, the phosphatic infill of the chambers of some proximal–distal pairs of autozooecia are linked by a thread which may represent the cast of a communication pore (Fig. 23c, d).

Regenerated mural rims are uncommon and have been observed only in non-caudate auto-zooecia. Some of the caudate autozooecia are occluded by smooth convex closure plates (Fig.

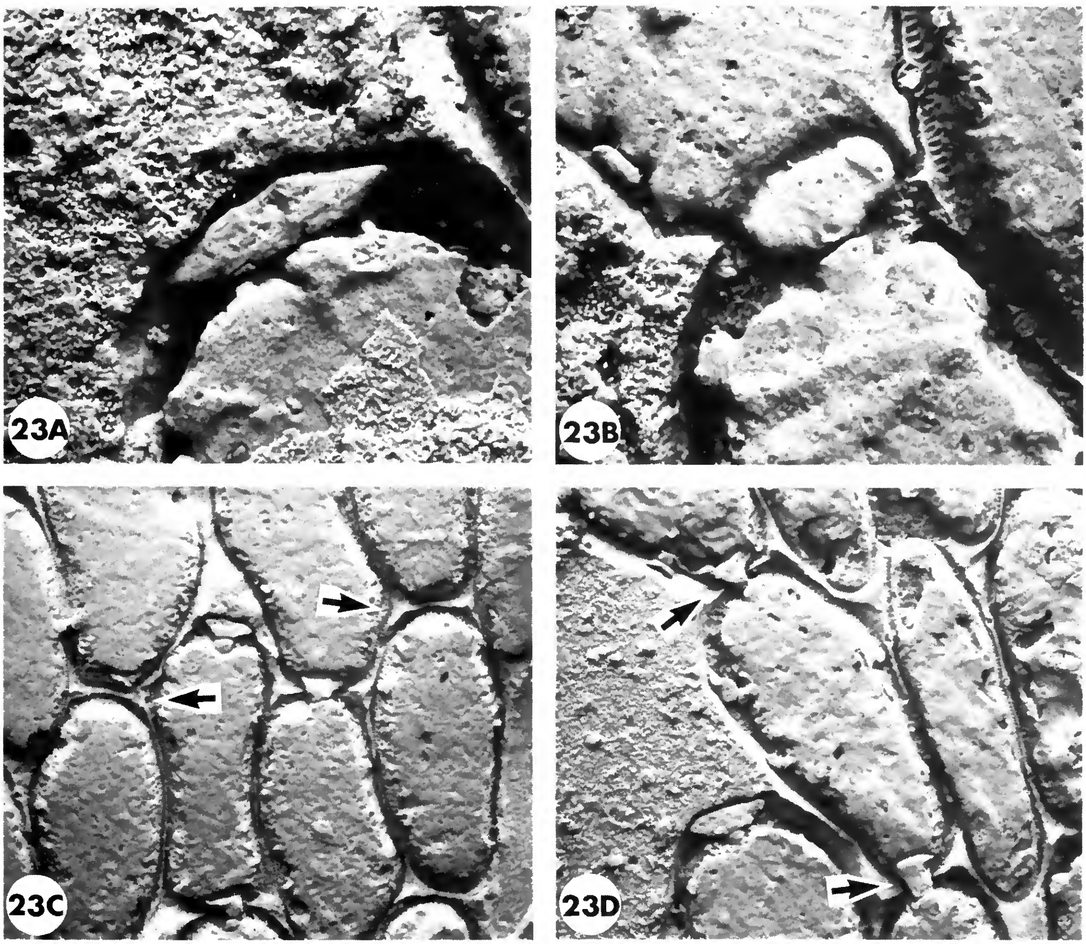


Fig. 23 *Spinicharixa dimorpha* gen. et sp. nov.; BMNH D35361, paratype; Gault Clay (Albian); Dunton Green, Sevenoaks, Kent; phosphatic moulds of undersides of zooecia with pore chambers; 23A, well-defined distal pore chamber in an autozooecium slightly more advanced in ontogeny than that depicted in Fig. 20B, × 190; 23B, distal pore chamber with an ill-defined distal exterior wall in an autozooecium still more advanced, × 190; 23C, autozooecia apparently lacking pore chambers in their distal transverse walls (arrows), together with others in which the distal pore chambers are still visible, × 48; 23D, autozooecia linked by phosphatic threads (arrows) suggesting open interzooidal pores between zooecia in proximal-distal series, × 64.

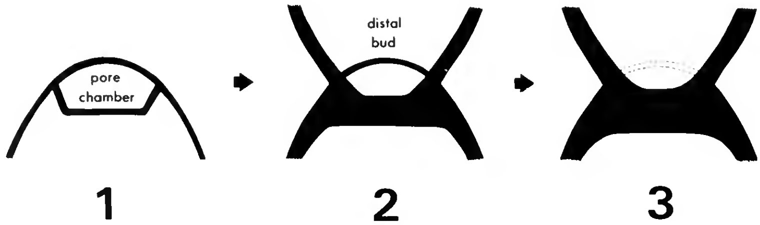
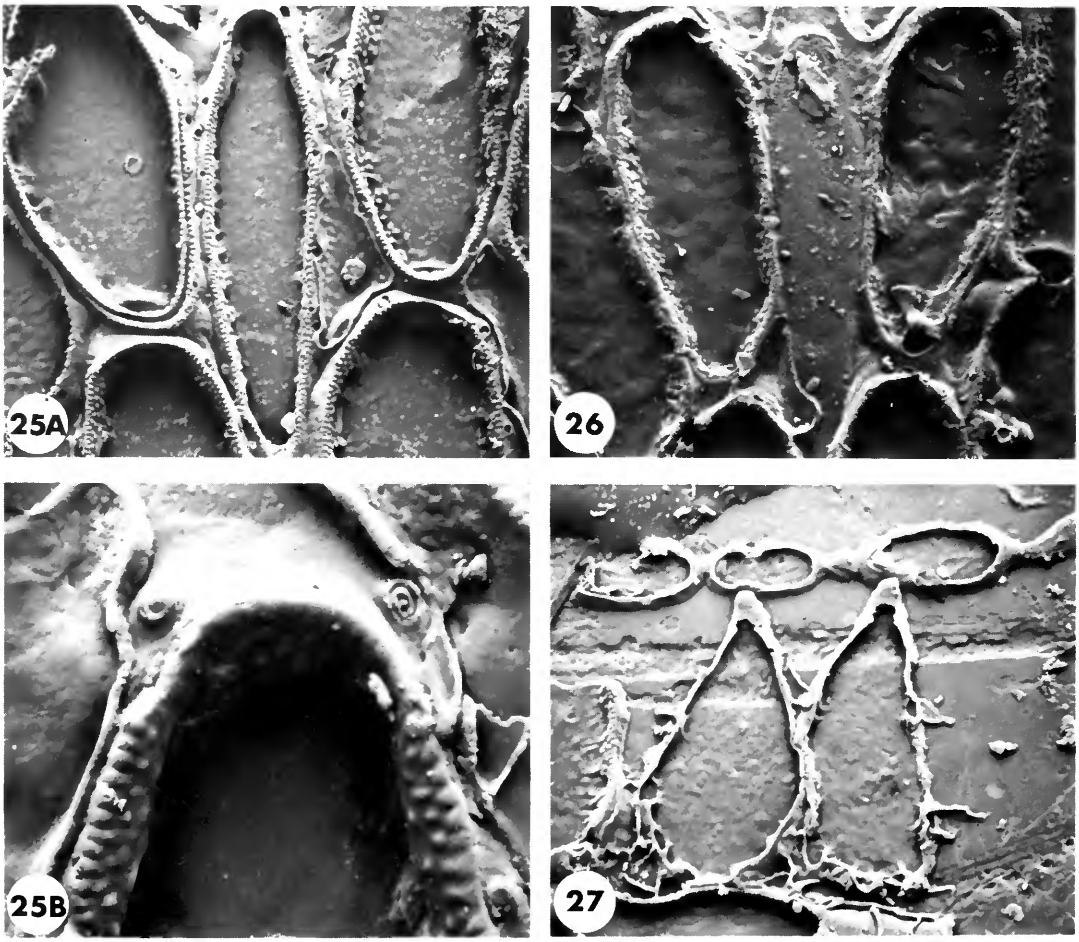


Fig. 24 Diagram of the apparent ontogeny of a distal pore chamber in *Spinicharixa dimorpha* gen. et sp. nov. Sequence inferred from phosphatic moulds in which only the basal outlines of the structures are generally visible; any interzooidal pores located above basal level are not visible in the sequence shown. Initially (Stage 1), the curved exterior wall of the pore chamber and the interior wall (septulum) are thin. Concurrently with the budding of a distal zooid from the pore chamber (Stage 2), all walls are thickened by calcification except for the curved length of exterior wall which is now enclosed by the newly budded zooid. Finally (Stage 3), this curved length of exterior wall is resorbed so that the two zooecia in lineal series are separated only by the thickened septulum.



Figs 25–27 *Spinicharixa dimorpha* gen. et sp. nov.; Gault Clay (Albian); latex casts prepared from phosphatic moulds. Fig. 25, BMNH D53152a, **holotype**; Naccolt Brickworks, Ashford, Kent; 25A, elongate opesiae of a caudate autozooecium, × 82; 25B, distal spine bases of a caudate autozooecium, × 370. Fig. 26, BMNH D35361, paratype; Dunton Green, Sevenoaks, Kent; caudate autozooecium with a closure plate, × 66. Fig. 27, BMNH D53152b, paratype; apparent bipolar pair (top) of astogenetically early autozooecia each budding a large, incompletely formed autozooecium orientated at right angles, × 70.

26) which occasionally bear a pair of crescentic impressions, about 0·10 mm apart, left by the opercular sclerites (Fig. 21). Closure plates have not been observed in non-caudate autozooecia.

Early astogenetic autozooecia are preserved in colony D53152b, in which the colony origin can be traced to two small autozooecia joined proximally and growing in opposite directions (Fig. 27). One is about 0·24 mm long, the other 0·33 mm long. The smaller of the two has a slight V-shaped notch in its proximal gymnocyst from which the larger autozooecium appears to emerge. This structure suggests fracturing of the proximal part of the smaller autozooecium to produce the V-shaped notch, followed by regenerative growth of an oppositely orientated bud from the fracture to give a 'bipolar pair' of zooecia (Taylor 1986). Although it is conceivable that the smaller of the two autozooecia is the ancestrula, the ancestrula and other astogenetically earlier autozooecia may have been removed during fracturing. Each of the two autozooecia have small distal buds and much larger lateral or distolateral buds orientated at right angles to their parent autozooecia (Fig. 27). A poorly-preserved but apparently similar bipolar pair is present in D55066, involving autozooecia of an astogenetically 'mature' size.

Kenozooecia (Figs 25a, 26) occupy some of the irregular spaces between autozooecia and overlap slightly onto the gymnocysts of the autozooecia. They are polygonal in outline, open and relatively featureless, seeming to lack cryptocyst, significant gymnocyst and spine bases.

Ovicells and avicularia are absent.

REMARKS. *S. dimorpha* is readily distinguished from previously described species by the dimorphism of the autozooecia and the characteristic growth pattern in which non-caudate autozooecia fill in the areas between lineal series of caudate autozooecia. The growth is similar to that found in some colonies of Recent species of *Electra* and *Conopeum*. Suboptimal diet has been shown to produce this growth pattern in colonies of *C. tenuissimum*, whereas well-fed colonies grow in compact sheets (Winston 1976). However, the growth pattern is species-characteristic in *Electra* and not ecophenotypic.

Table 1 Zooecial dimensions (mm) determined from a minimum of ten autozooecia for each of seven species of *Charixa* and *Spinicharixa*.

	zl	zw	ol	ow
C. vennensis (p. 201)				
$\bar{x}$	0·51	0·24	0·24	0·14
SD	0·134	0·043	0·038	0·024
r	0·21–0·66	0·18–0·32	0·17–0·27	0·11–0·18
C. lhuydi (p. 203)				
$\bar{x}$	0·44	0·33	0·31	0·22
SD	0·039	0·032	0·039	0·023
r	0·38–0·50	0·30–0·39	0·24–0·36	0·18–0·26
C. cryptocauda (p. 205)				
$\bar{x}$	0·53	0·24	0·33	0·16
SD	0·056	0·039	0·029	0·027
r	0·44–0·62	0·18–0·32	0·29–0·39	0·12–0·21
C. lindiensis (p. 208)				
$\bar{x}$	0·41	0·20	0·27	0·13
SD	0·034	0·023	0·033	0·017
r	0·36–0·45	0·17–0·24	0·21–0·32	0·11–0·17
C.? sp. (p. 208)				
$\bar{x}$	0·72	0·34	0·42	0·21
SD	0·057	0·045	0·052	0·040
r	0·66–0·84	0·30–0·45	0·32–0·48	0·15–0·27

	zl	zw
S. pitti (p. 210)		
$\bar{x}$	0·41	0·25
SD	0·027	0·037
r	0·36–0·45	0·20–0·35
S. dimorpha: non-caudate (p. 215)		
$\bar{x}$	0·92	0·36
SD	0·099	0·036
r	0·80–1·11	0·29–0·41
S. dimorpha: caudate (p. 215)		
$\bar{x}$	1·35	0·26
SD	0·096	0·019
r	1·16–1·50	0·21–0·29

Abbreviations: zl, zooecial length; zw, zooecial width; ol, opesial length; ow, opesial width; $\bar{x}$, mean; SD, standard deviation; r, observed range.

There are sufficient differences between *S. dimorpha* and the type species of *Spinicharixa*, *S. pitti*, to suggest that assignment to a separate genus may be appropriate when more is known of primitive anascans.

Distribution. M. Albian (*loricatus* Zone, *intermedius* Subzone)–U. Albian (*inflatum* Zone, *orbignyi* Subzone) Gault Clay of Kent, England.

Discussion

The established stratigraphical range of cheilostome bryozoans extends from the Upper Jurassic to the Recent. During approximately the first third of their history, until the late Albian, cheilostomes remained morphologically simple and conservative, and were taxonomically depauperate. They were uncommon in terms of numerical abundance, despite attaining a widespread geographical distribution with a broad palaeolatitudinal range.

The majority of pre-late Albian cheilostomes had uniserial, pluriserial or loosely-organized multiserial colonies in which interzooidal communication between zooidal series was lacking or very restricted. The Polish Valanginian–Hauterivian species *Wawalia crenulata* is an exception in having tightly-packed zooecia forming multiserial colonies in which regular communication pores apparently linked zooids in adjacent series (Dzik 1975: fig. 3a). All early Cretaceous species known from adequately preserved material appear to have pore chambers; failure to record pore chambers in some species may be owing to poor preservation and perhaps also to their resorption in ontogenetically older zooids (cf. *Spinicharixa dimorpha*, p. 217). Budding was intrazooidal (*sensu* Lidgard 1985). Opesiae are extensive and bordered by steeply sloping cryptocysts which are little more than outwardly flared continuations of vertical walls. Cryptocysts are ornamented by pustules (e.g. *Spinicharixa*), radial striae (*Pyriporopsis*) or striae which break into pustules towards the centre of the zooid (*Wawalia*). The boundary between the cryptocyst and the surrounding gymnocyst is ill-defined, crenulated and does not involve a significant change in vertical relief (cf. *Wilbertopora* where the outer edge of the cryptocyst is raised above the level of the gymnocyst). Proximal gymnocysts are moderately to well developed, especially in uniserial species which may have distinctly caudate zooids. Spine bases occur regularly in some species (*Spinicharixa* spp.) and sporadically in others (e.g. *Charixa lindiensis*, *Pyripora texana*). Regular spine bases can be large and may indent the margin between gymnocyst and cryptocyst, whereas sporadic spine bases are small, paired and distally situated ('orificial'). Kenozooecia may be found in most or all species and apparently represent zooids budded into irregular and restricted spaces. Unequivocal ovicells and avicularia have not been described in pre-late Albian cheilostomes.

A significantly more advanced morphological grade first appears in the late Albian species *Wilbertopora mutabilis* from the U.S.A. (Cheetham 1954, 1975), together with a few poorly described species (e.g. '*Membranipora*' *elliptica* (?) Hagenow of Vine, 1890*a*) from the contemporaneous Red Chalk of Britain, which have ovicells and avicularia. The great majority of anascans involved in the late Cretaceous radiation of the Cheilostomata were also species with ovicells and avicularia. The attainment of this grade of organization may have considerable relevance to the diversification of cheilostomes during the late Cretaceous.

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Miscellanea II

Contents

New material of the plesiosaur *Kimmerosaurus langhami* Brown from the Kimmeridge Clay of Dorset

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Synopsis

New specimens of the Kimmeridgian cryptoclidid plesiosauroid *Kimmerosaurus langhami* Brown provide additional data on the morphology and ontogeny of the skull, and the anterior cervical vertebrae are newly described. An emended diagnosis is given and the possibility of the synonymy of *Kimmerosaurus* with the 'elasmosaur' *Colymbosaurus*, the only other British Kimmeridgian plesiosauroid, is considered.

Introduction

Kimmerosaurus langhami was described by Brown (1981) on the basis of a single partial skull, Department of Palaeontology, British Museum (Natural History) register no. R.8431. A second specimen, consisting of a braincase, mandible and anterior cervical vertebrae, collected by P. A. Langham in 1976 and at that time in the private collection of R. A. & P. A. Langham, was referred to *K. langhami* by Brown, but was not available for description. This material has subsequently been presented to the Department by R. A. Langham, where it is registered as R.10042. A third specimen (R.1798), a previously unidentified fragmentary skull purchased from the executors of R. Damon in 1890, also belongs to *K. langhami.* These two additional specimens provide further data on skull morphology, ontogenetic changes of the skull and the first record of vertebrae in *Kimmerosaurus.*

The material described herein is housed in the collections of the British Museum (Natural History) (specimen numbers prefixed by R or without prefix), the Sedgwick Museum, Cambridge (SMC) and the Hunterian Museum, University of Glasgow (GLAHM).

Description

Order **PLESIOSAURIA** de Blainville, 1835

Superfamily **PLESIOSAUROIDEA** (Gray, 1825) Welles, 1943

Family **CRYPTOCLIDIDAE** Williston, 1925

Genus ***KIMMEROSAURUS*** Brown, 1981

TYPE SPECIES. *Kimmerosaurus langhami* Brown, 1981 (monotypic genus).

EMENDED DIAGNOSIS. Tooth ornament absent; teeth greatly recurved, sharply pointed and labiolingually compressed; premaxilla bears at least eight teeth; dentary bears 36 teeth; parietals do not form a sagittal crest; quadrate overlaps quadrate ramus of pterygoid antero-laterally; paroccipital process of exoccipital-opisthotic is relatively short and massive; occipital condyle not ringed by a groove and extends onto pedicels of the exoccipitals; vertebrae have relatively amphicoelous centra, the shape of a cross section of the articular face being a double sigmoid curve; length of anterior cervical centra less than height. (The postcranial skeleton is known only from anterior cervical vertebrae.)

Kimmerosaurus langhami Brown, 1981

HOLOTYPE. Partial skull and mandible (R.8431).

TYPE LOCALITY. 250–270 m west of Freshwater Steps, to the west of Egmont Bight, Isle of Purbeck, Dorset (National Grid reference SY 942773).

REVISED HORIZON. The specimen was recovered from a detached block of shale coming from about 2 m above the Middle White Stone Band, and is therefore from the upper part of the *eastlecottensis* Subzone, *pectinatus* Zone, Upper Kimmeridge Clay, Kimmeridgian Stage, Upper Jurassic (Cope *et al.* 1980; Cox & Gallois 1981). The horizon was incorrectly given as *rotunda* Zone by Brown (1981: 301).

REFERRED SPECIMENS. R.1798: partial skull and mandible; Kimmeridge Clay; Weymouth (no detailed data available but the specimen almost certainly came from a cliff exposure between Sandsfoot Castle and the old Portland Ferry Bridge described by Damon, 1884).

R.10042: partial skull and mandible, atlas-axis and five cervical vertebrae; from the type locality and horizon, *in situ* about 3 m east of the site of R.8431; collected P. A. Langham, 1976.

Description of skull material

The skull of R.10042. The preserved parts of this skull are the posterior region of the left mandibular ramus including the sockets for the last 15 teeth; a smaller portion of the right mandibular ramus posterior to the tooth row; and a part of the braincase comprising the basioccipital, both exoccipital-opisthotics, the supraoccipital and the basisphenoid.

The left mandibular ramus has undergone some post-mortem straightening, the ventral margin being now almost straight, whereas this is seen in the undistorted holotype skull (R.8431; Brown 1981: figs 28, 38) to show a substantial curvature. In all other features it agrees with the holotype. The angular has fused with the always fused surangular-articular, and posteriorly the position of the closed suture is harder to trace. When the tooth row is laid against that of R.8431 it is found that the 15 tooth sockets of R.10042 occupy the same length as the posterior 17 sockets of R.8431, indicating that the new specimen was a slightly larger individual. Unlike the holotype, the dentary is preserved in full articulation with the posterior elements (Fig. 1). In lateral view the posterior margin of the dentary lies posterior to the highest elevation of the coronoid process, and the most posterior tooth socket is only just in advance of the coronoid process. Brown's lateral reconstruction of the holotype (1981: fig. 29) shows the coronoid process about 15 mm posterior to its true position.

The braincase was preserved compressed around the posterior end of the right mandibular ramus. During preparation the mandible was separated, and only a small fragment of the end

Fig. 1 *Kimmerosaurus langhami* Brown, R.10042. Posterior part of left ramus of mandible in dorso-lateral aspect, × 0·6. A, angular; ART, articular; D, dentary; SA, surangular.

of the retroarticular process now remains attached to the braincase floor (Fig. 2). The elements are somewhat distorted by crushing, and on the right side the basipterygoid process of the basioccipital has been displaced upwards and outwards so that part of the base now covers the jugular foramen of the right exoccipital-opisthotic. On the left side these fused elements and the basipterygoid process are much better preserved.

The basioccipital and exoccipital-opisthotics are fully fused, and the line of fusion cannot be traced. However, the edge of the articular surface of the occipital condyle shown in Fig. 2 extends dorsolaterally to form a lip running onto the assumed region of the pedicles of the exoccipitals, indicating that those elements have a role in the formation of the condyle, a feature of taxonomic importance. The condyle is thus not ringed by a groove. However, it shows two differences from that of the holotype: there is no notochordal pit, so that the condyle has a more spherical shape; and the dorsal edge of the condyle is convex, being slightly elevated above the level of the floor of the foramen magnum (whereas in R.8431 the concave floor of the foramen forms its dorsal margin).

The general shape and orientation of the basipterygoid process of the basioccipital are as in the holotype, but the cartilage-covered area associated with the articular surface for the pterygoid is elliptical in shape and extends further anteromedially than in R.8431. It is separated from the basisphenoid only by a very narrow strip of periosteal bone, whereas in R.8431 the articular surface is more nearly circular and separated from the basisphenoid facet by 8 mm on the right and 11 mm on the left. All other features of the basioccipital and exoccipital-opisthotic are extremely similar to those of the holotype, and in particular the taxonomically important paroccipital process, complete on the left side, agrees in all details.

The basisphenoid and supraoccipital (Fig. 2) have not been described previously as they are absent from R.8431. The basisphenoid is fused to the basioccipital, the position of the spheno-occipital synchondrosis being still discernible dorsally on the floor of the braincase as a transverse shallow groove (partly hidden by the mandibular fragment) but obliterated ventrally. It differs slightly from those of *Muraenosaurus* and *Tricleidus* (described and figured by Andrews 1910: text-figs 44, 73) in the relative proportions of the body to the hypophyseal ('pituitary') fossa. The body appears to be very short in the axial dimension, and the hypo-

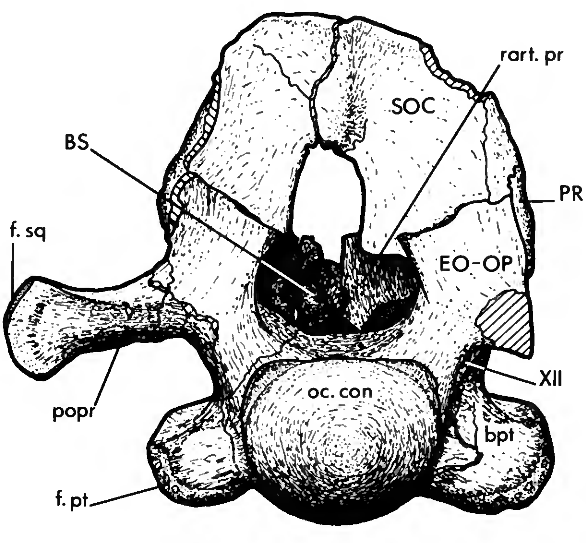


Fig. 2 *Kimmerosaurus langhami* Brown, R.10042. Occipital view of braincase, natural size. bpt, basipterygoid process of basioccipital; BS, basisphenoid; EO-OP, exoccipital-opisthotic; f.pt, facet for pterygoid; f.sq, facet for squamosal; oc. con, occipital condyle; popr, paroccipital process of exoccipital-opisthotic; PR, prootic; rart. pr, retroarticular process of mandible; SOC, supra-occipital; XII, foramen for hypoglossal nerve (hypoglossal canal).

physial fossa relatively large. The bone of the floor of the fossa probably consists of basisphenoid with the parasphenoid fused beneath, as very clearly shown in Andrews' figure of *Tricleidus*. The internal carotid foramen is visible on both sides and, on account of the shortness of the basisphenoid body, appears relatively close to the base of the basipterygoid process. On the right side, in advance of the internal carotid foramen, a process of bone ascends to form a contact with the anterior prolongation of the prootic as was described by Andrews (1910) for *Tricleidus* and *Cryptoclidus*.

The supraoccipital resembles in its general shape those of *Muraenosaurus* and *Cryptoclidus* (Andrews 1910: text-fig. 45; pl. 9). It encloses the upper half of the foramen magnum, which is somewhat restricted in diameter at the position of the supraoccipital–exoccipital union. Thus an aperture of almost circular shape is two-thirds surrounded by the basioccipital and exoccipitals but is then extended upwards between the arches of the supraoccipital so that the final shape is irregular, with the greatest diameter in the sagittal plane (see Fig. 2). A ridge or low crest is present in the midline of the occipital surface above the foramen magnum, similar to that seen in *Muraenosaurus* (Andrews 1910: text-fig. 45A). Andrews suggested that the end of this ridge may have projected into the foramen magnum, but his figure is incorrectly orientated, and by tilting the upper edge of the supraoccipital forwards, this 'apparent' projection is eliminated. In R.10042 the supraoccipital is still orientated in approximately the correct plane with reference to the basioccipital.

The supraoccipital itself is rather thin and flat. Dorsally it forms a single facet for the parietal which is slightly crescentic and very elongated transversely (transverse length 37 mm, greatest width 7 mm). As in *Cryptoclidus* (Andrews 1910: pl. 9; text-figs 1, 4) the parietal facet is separated by an area of convex periosteal bone margin (5 mm in the present specimen) from the anteroventrally-directed area of union with the prootic. The latter region is broken on both sides; but the appearance, especially on the right side where the remains of a closed suture may be visible, suggests that the supraoccipital and prootic were fused in this specimen.

The skull of R.1798. This specimen consists of an incomplete mandible in several pieces together with the squamosals and associated fragments of the quadrates, jugals and postorbitals.

The mandibular tooth row is preserved intact on the right side from the symphysis to the back of the 24th tooth socket. The distance from the median posterior surface of the symphysis to the lingual surface of the back of the right tooth row is 135 mm. On the left side, the ventral margin of the mandible is preserved but there is a large gap in the middle of the tooth row. However, by measuring 135 mm from the symphysis the position of the 24th socket can be determined, and behind this are a further 11 sockets to the back of the tooth row as preserved, bringing the observable count to 35. The dentary behind this point is missing, but on the deep surface of the posterior part of the dentary is seen a shallow depression for the squamous overlap of the surangular. When this same shallow depression is examined in the holotype disarticulated dentary and its relationship to the tooth row noted, the posterior last few sockets of both specimens may be compared, and it appears probable that only one or at the most two further sockets are needed to complete the mandibular tooth row. This gives a count of 36 or 37 in R.1798 which compares with 36 in R.8431.

The posterior elements of the mandible (angular and fused surangular-articular) are preserved on the right side, and are about the same size as in R.10042, being again a little larger than the holotype. The surangular extends 30 mm further anterior to that of R.10042, but its lateral surface bears a shallow depression showing the posterior extent of the dentary, which confirms that the relative positions of the back of the tooth row and of the jaw joint were exactly as in the other two specimens. Similarly, the angular and surangular-articular are fully fused.

In so far as they are preserved, the squamosals and quadrates, conform to the structure of those elements in the holotype. The facet for articulation with the paroccipital process of the opisthotic is well seen on the left side. The ventral extremities of the pterygoid facets of the quadrates are present, and on the left side the tip of the quadrate process of the pterygoid

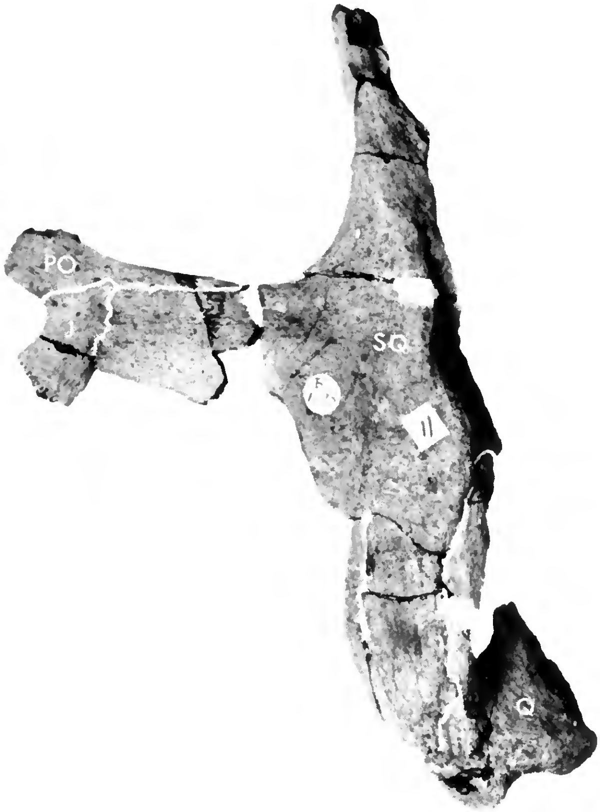


Fig. 3 *Kimmerosaurus langhami* Brown, R.1798. Fragment of left cheek in lateral aspect, × $\frac{2}{3}$. J, jugal; PO, postorbital; Q, quadrate; SQ, squamosal.

appears fused onto this surface, showing the diagnostic manner of union of these elements. In R.8431 the anterior ramus of the squamosal on both sides terminates at the sutural surface, but on R.1798 posterior fragments of the postorbital and jugal elements remain attached, and anteriorly between these elements, on both sides, a part of the margin of the orbit is preserved. The orbital margin is only 12 mm anterior to the middle of the suture on the squamosal.

The left jugal fragment is the better preserved (Fig. 3), and consists of a thin strap-like element which runs sharply downwards from the squamosal, the ventral margins of the elements forming an obtuse angle of about 100°. The jugal and postorbital are fused, but the outline of the once-discrete left jugal is still clearly visible on the lateral surface of the left side, occupying the lower four-fifths of the anterior end of the squamosal. The postorbital unites with the dorsal end of the jugal and the remaining one-fifth of the end of the squamosal, then extends posteriorly above the squamosal for a distance of 25 mm. In medial aspect, the fused postorbital and jugal are seen to overlap the squamosal more extensively, running from the posterodorsal corner of the postorbital to the ventral obtuse angle between the squamosal and jugal in an almost straight line. On the medial aspect of the right side, the appearance of the broken upper end of the postorbital suggests that it probably continued towards the parietal as the posterior component of the postorbital bar. On the left side the appearance is similar, and in addition there is another process of bone, presumably of the postorbital, which passes anteriorly for about 7 mm and probably would have made contact with the postfrontal. The lower edge of this process forms part of the margin of the orbit, and meets the dorsal margin of the jugal at a rounded-out angle of rather less than 90° to form the posterolateral corner of the orbit.

Discussion. The skulls of R.10042 and R.1798 are of almost identical size, as is shown by the comparison of the mandibular fragments, the only parts to be preserved in both. They are very slightly larger than the holotype skull R.8431. Of the diagnostic characters of *Kimmerosaurus langhami* listed by Brown (1981) and above, the number of mandibular teeth (36 in R.8431) is fairly reliably estimated as 36 or 37 in R.1798, in which specimen also the quadrate is seen to overlap the quadrate ramus of the pterygoid anterolaterally. The paroccipital process of the exoccipital-opisthotic in R.10042 has exactly the same short and massive structure as in R.8431 (representing an extreme of development amongst the Plesiosauroidea). Although the basioccipital and exoccipital-opisthotic are fused in R.10042, their appearance in the specimen nevertheless confirms the formation of the occipital condyle in this genus and species from both elements. Thus the identification of the specimens is determined; there now remain, however, several differences between R.10042 and the holotype to be explained.

Almost all the differences are accounted for by reference to ontogeny. R.10042 is not only slightly larger than the holotype R.8431 but also ontogenetically a little older because it shows a greater degree of fusion between the elements. The suture between the angular and the surangular-articular is harder to trace; the dentary is preserved in full articulation with the posterior mandibular elements, whereas in R.8431 it was more loosely attached and was preserved disarticulated. The basioccipital and exoccipital-opisthotic are fully fused with complete obliteration of the synchondrosis and, similarly, the spheno-occipital synchondrosis is largely closed, whereas all the braincase elements recovered in R.8431 were disarticulated. In view of this weight of evidence that R.10042 represents an individual older than R.8431, it seems reasonable to suppose that the lack of a notochordal pit in the occipital condyle of R.10042 is also an ontogenetic difference, the late-lingering embryonic remnant seen in R.8431 being eventually eliminated.

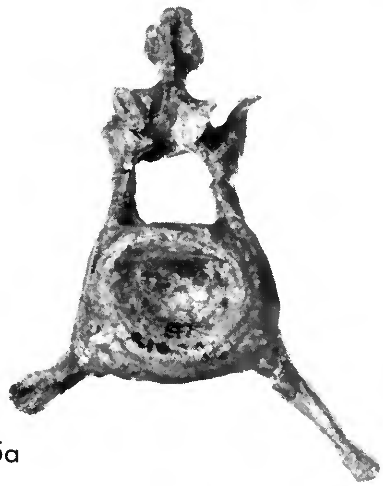
One other difference between R.10042 and R.8431, the greater extent of cartilage-covered surface on the basipterygoid process of the former, still requires explanation. The condition in R.10042 more closely resembles that seen in the genera *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*, in which the pterygoid and basisphenoid facets of the basioccipital show confluence of cartilage in all but the most fully-ossified 'old adult' specimens (Brown 1981). The difference between the specimens is thus contrary to expectations based upon ontogeny, and it may therefore be that the holotype is atypical in this regard.

Finally, the preservation of fragments of the jugal and postorbital associated with the squamosal in R.1798 (the relationship of the orbital margin can be seen in Fig. 3) demonstrates that the arrangement of this region of the skull as tentatively reconstructed by Brown (1981: fig. 29) is broadly correct. In particular, the orientation of the jugal as a narrow near-vertical bar forming parts of both the orbit margin and the ventral margin of the cheek, not typical of plesiosaurs generally, is confirmed by this specimen.

Description of vertebrae

The fused atlas-axis and five anterior postaxial cervical vertebrae are preserved with R.10042. This is the only postcranial material yet discovered in association with diagnostic skull material of *Kimmerosaurus langhami*. There can be no proof that the disarticulated vertebrae are serial, but direct evidence that they are all from the very anterior end of the neck is provided by the neural spines. On the sides of the neural spines, just below their tips, are well-developed excrescences which arise behind the anterior edge of the spine and form oblique ridges which run posterodorsally and increase in elevation to terminate abruptly near the posterior margin of the spine. In the neotype of *Cryptoclidus eurymerus* (Phillips) (R.2860) and the holotype of *Muraenosaurus leedsii* Seeley (R.2421), which are adult specimens, have complete necks and represent distinct families (Cryptoclididae and Elasmosauridae respectively), these same excrescences occur only on the neural spines of the first five or six postaxial vertebrae. They were probably, therefore, associated with the attachment of muscles or slips of nuchal ligament involved in supporting the dorsal part of the occiput. When placed together the postaxial vertebrae appear to comprise a good series and have therefore been numbered 3–7 (Fig. 4).

4



5a

5b

6a

6b

Figs 4–5 *Kimmerosaurus langhami* Brown, R.10042. Fig. 4, postaxial cervical vertebrae placed in series 3–7 from left to right, × $\frac{2}{3}$. Fig. 5, cervical vertebra 4, × $\frac{3}{4}$: a, posterior; b, left lateral aspect.
Fig. 6 *Colymbosaurus trochanterius* Owen, R.10062. Anterior cervical vertebra, × $\frac{3}{4}$: a, posterior; b, left lateral aspect.

The atlas-axis has the usual adult form, with all the component elements fused. The atlas–neural arch outline can still be distinguished, but the atlas intercentrum cannot. Both atlas and axis ribs were fused and are now broken off and missing. In all respects the complex is indistinguishable from the atlas-axis of *Cryptoclidus eurymerus*; fusion of component parts beyond that seen in R.2860 (Andrews 1910: text-fig. 78C, D) indicates again that this is an 'old adult' specimen.

The neural arches and cervical ribs of the postaxial vertebrae are fully fused. In addition to the excrescences on the neural spines, already described, a horizontal rugose ridge runs antero-posteriorly across the side of the anterior zygapophysis and neural arch pedicle, a feature which was also noticed in anterior vertebrae of *Cryptoclidus* and *Muraenosaurus*. All the cervical ribs are damaged and it is not possible to describe their exact shape or make comparisons.

The anterior cervical centra of plesiosaurs show three characters of importance in taxonomy: the presence or absence of a lateral keel (lateral longitudinal ridge, lateral crest *auctt.*); the shape of the anterior face; and the proportional length of the centrum. The latter character is, for comparative purposes, expressed as a vertebral length index (VLI), which is calculated as the vertebral length (l) divided by the average of posterior central width (w) and height (h), × 100 (Brown 1981). In R.10042 the lateral keel is absent (Fig. 5), and the articular face is deeply concave, the shape of the transverse section being a double sigmoid curve because the margins of the face are convex. The measurements of the centra of R.10042 are given below. Also given are corresponding figures for three 'adult' specimens of *Colymbosaurus trochanterius* (Owen): 40106 (holotype of *Plesiosaurus manselii* Hulke, synonymized with *C. trochanterius* by Brown, 1981); SMC J.29596 etc. (syntype of *Plesiosaurus megadeirus* Seeley, also synonymized with *C. trochanterius* by Brown, 1981); and R.10062 (Fig. 6), a recently collected specimen from the Isle of Portland, reported by Brown, 1984.

In *Kimmerosaurus* R.10042 the length index of the atlas-axis is more than 20% less than in *Colymbosaurus* 40106 and SMC J.29596 etc. Similarly, the average vertebral length index for the first five postaxial vertebrae is only 66·6, and so these are proportionally 20% shorter than in SMC J.29596 etc. In *Colymbosaurus* 40106 there is a gap in the sequence of vertebrae preserved from the axis to about the twelfth cervical, and so comparison between the most anterior postaxial cervical vertebrae of that specimen and R.10042 cannot be made. In R.10062 the neck is very incomplete and only one very anterior cervical, showing lateral excrescences on the neural spines, has been found (Fig. 6). This vertebra has dimensions between those of cervicals 3 and 4 (Fig. 5) of R.10042, and its vertebral length index is only 67·9, almost exactly the same as the average (67·3) of those two vertebrae in R.10042.

Table 1 Measurements of anterior cervical vertebrae (mm). l = vertebral length; w = posterior central width; h = posterior central height. VLI = vertebral length index (l × 100 ÷ (w + h)/2); see text. (E) = estimated.

1. R.10042		l	w	h	VLI
Atlas-axis	crushed laterally	35·9	*31·6	*25·2	126·4
Cervical 3	good condition	18·8	34·8	27·0	60·8
Cervical 4	posterior face chipped	24·7	38(E)	28·9	*c.* 73·8
Cervical 5	good condition	25·6	44·0	33·2	66·3
Cervical 6	crushed longitudinally	28(E)	46·5	40·4	*c.* 64·4
Cervical 7	crushed vertically	31·4	47·7	45(E)	*c.* 67·7
2. Specimens of *C. trochanterius*		**l**	**w**	**h**	**VLI**
40106	atlas-axis	45·8	33·0	26·8	152·3
SMC J.29596 etc.	atlas-axis	44·7	30·0	26·8	163·1
R.10062	'anterior' cervical	21·8	36·0	28·2	67·9
SMC J.29596 etc.	cervical 5	27·9	36·2	30·2	84·0

* w and h are anterior face of cervical 3.

Discussion. Brown (1981) recognized two species of Upper Jurassic plesiosauroids from the Kimmeridge Clay of England and referred them to two monotypic genera. One of those is *Kimmerosaurus langhami* Brown 1981, hitherto known only from cranial material; its skull is the most lightly built of all species in the Upper Jurassic. The other is *Colymbosaurus trochanterius* (Owen 1840) known only from five incomplete skeletons and a number of isolated propodials; it is the longest English plesiosauroid (> 6 m) and the most massively built. Brown referred the two genera to different families, *Kimmerosaurus* to the Cryptoclididae of Williston and *Colymbosaurus* to the Elasmosauridae of Cope.

The only elements known in both genera are the anterior cervical vertebrae (in *Kimmerosaurus* only in specimen R.10042); they are closely similar, especially with regard to the posterior height and width of the centra and the form of the articular facet. *Colymbosaurus* and *Kimmerosaurus* might therefore be synonyms for a genus of plesiosauroid with a lightly built delicate skull and a specialized fine slender dentition. If that were true, it would affect the choice of criteria by which the families Cryptoclididae and Elasmosauridae might be distinguished.

The elasmosaurids are typified by elongated necks, produced by increases both in the number of cervical vertebrae and in the proportional lengths of the individual centra, especially the anterior cervicals. Further, according to Brown, their anterior cervical centra are generally equipped with a lateral keel and an articular face which has either a single shallow concavity or an open V-shape. The cryptoclidids, by contrast, do not have elongated necks (the number of cervical vertebrae remaining at the primitive figure of 30–32); their anterior cervical centra do not have lateral keels; and the articular faces of those centra show a deep concavity with a convex rim. They share certain characters of the dentition and occiput.

Of the plesiosauroid genera in the Middle and Upper Jurassic of England, *Muraenosaurus* is a typical elasmosaurid—though with its neck less elongated than in Cretaceous elasmosaurs. The anterior cervical vertebrae of *Tricleidus* and *Colymbosaurus*, though those genera are included by Brown (1981) in the Elasmosauridae, lack lateral keels and possess an articular face shape like those of cryptoclidids. Brown referred *Tricleidus* to the elasmosaurids only because of certain characters of the dentition and occiput, and *Colymbosaurus* was included only because of its augmented cervical count (42).

Measurement of the average VLI of cervical vertebrae 3–7 of the above plesiosauroids and of *Kimmerosaurus* R.10042 provides useful comparative data. Values, in descending order of relative length of centra, are as follows:

'adult' *Muraenosaurus* (R.2421)	95·1;
'adult' *Tricleidus* (R.3539)	93·7;
'old adult' *Cryptoclidus* (GLAHM V.1091)	88·8;
'adult' *Colymbosaurus* (SMC J.29596 etc.)	84;
'old adult' *Kimmerosaurus* (R.10042)	66·6 (VLI is increased with ontogeny).

These figures show that, with regard to proportional length of anterior cervical centra, *Colymbosaurus* falls within the same range as *Cryptoclidus*, whereas in *Kimmerosaurus* R.10042 these vertebrae are proportionally 20% shorter. A similar degree of difference is found between the VLI of the atlas-axis in *Colymbosaurus* and *Kimmerosaurus* R.10042. Since this difference is greater than the margin separating 'adult' *Muraenosaurus* and 'old adult' *Cryptoclidus*, the measurements suggest that *Colymbosaurus* and *Kimmerosaurus* are very distinct. However, the dimensions and VLI of the only known anterior cervical of *Colymbosaurus* R.10062 fall between the values for cervicals 3 and 4 of *Kimmerosaurus* R.10042, and those vertebrae of the two individuals are indistinguishable. Thus the evidence for synonymizing the genera is ambivalent.

A full description of R.10062 might throw further light on the problem of the status of the genera, and it is possible that cranial material of this specimen may yet be found. Discovery of a single associated tooth, for example, would end the debate. If *Kimmerosaurus* should prove to be a junior synonym of *Colymbosaurus*, then the skull characters of the enlarged genus would still show it to be a cryptoclidid, albeit with an independently derived increase in the number of cervicals. If not, then *Kimmerosaurus* would simply remain a cryptoclidid; but *Colymbosaurus* might still be an elasmosaurid because of its longer neck. Until such time as diagnostic associated skull and postcranial material is found, it is in the interest of stability of nomenclature to retain both names.

Summary

Two additional specimens of the Kimmeridgian cryptoclidid plesiosauroid *Kimmerosaurus langhami* Brown, identified and described with reference to the hitherto unique holotype, provide new data on osteology and ontogenetic changes of the braincase and cheek. The only known postcranial elements of *Kimmerosaurus* are the atlas-axis and anterior cervical vertebrae; the vertebrae are closely comparable with those of *Colymbosaurus*, a contemporary elasmosaurid known only from postcranial material. The possibility that *Kimmerosaurus* might be synonymous with *Colymbosaurus* is discussed, in which case *Colymbosaurus* would have to be reassigned at family level as a long-necked cryptoclidid. However, the evidence for synonymy is ambivalent and both names are currently retained pending the description of more complete material.

Acknowledgements

We should particularly like to thank Mr R. A. Langham for his generosity in donating (through Dr L. B. Halstead of the University of Reading and M.A.T.) the second specimen of *Kimmerosaurus langhami* (R.10042) to the collections of the British Museum (Natural History), and thus making it available for study. We are also indebted to Mr W. Lindsay for his skilled preparation of the braincase of R.10042; the Photographic Unit for Figs 1 and 3–6; and Mrs Wendy Ashurst, of the University of Newcastle upon Tyne, for photographic help in the preparation of Fig. 2. We also thank Dr A. J. Charig for his constructive criticism of the manuscript. D.S.B. gratefully acknowledges the assistance of Dr C. L. Forbes, lately of the Sedgwick Museum, Cambridge, and Dr J. K. Ingham of the Hunterian Museum, University of Glasgow, in his study of specimens in their care.

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Erratum

In Brown (1981: 263) the caption to fig. 4 is unfortunately incomplete as printed. The last sentence should read 'Sites of fusion between the articular, angular and surangular (indicated by broken lines) are discernible from bone growth-lines.'

Plant macrofossils from the Edgehills Sandstone, Forest of Dean

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Synopsis

The plant macrofossils in the Edgehills Sandstone (Carboniferous) represent a restricted 'flöznahe'-type flora, dominated by the equisete *Archaeocalamites radiatus* (Brongniart) and the lycopods *Tomiodendron variabilis* (Lele & Walton) and *Lepidostrobophyllum lanceolatum* (Lindley & Hutton). These species indicate that the Edgehills Sandstone is upper Viséan, rather than lower Westphalian as suggested on palynological evidence. It supports the view that from the late Viséan to the late Westphalian, the Forest of Dean was part of an area of non-deposition separating south Wales from the other sedimentary basins immediately south of St George's Land.

Introduction

Edgehills Quarry, near Mitcheldean, Forest of Dean (Grid Ref. SO 661168) exposes about 40 m of steeply dipping Carboniferous strata. Mostly, they are conglomerates and sandstones typical of the Drybrook Sandstone (Viséan), but the uppermost 5 m consists of rather fine sediments with a thin coal (the Edgehills Coal). Field observations suggest that these finer sediments are perfectly conformable with the Drybrook Sandstone (see Fig. 2) and a Viséan age would be assumed. However, spore floras reported from the coal seem to indicate an early Westphalian A age (Sullivan 1964, Spinner 1984). The only other palaeontological evidence available is a macroflora from the mudstone immediately underlying the coal. This is of limited composition but is sufficient to indicate an early Carboniferous (Mississippian) age. Since the age of the Edgehills Sandstone has a bearing on the general geological development of this part of Britain, a brief description of the macroflora is given here.

When Sullivan and Spinner collected their samples, there were two small quarries at Edgehills. Since then, the excavated area has been enlarged to form a single quarry. It is therefore important to justify the assumption that the macroflora came from the same level as the microflora. Fig. 3 is a map showing the positions of the old quarries relative to the new quarry, based on an old 1 : 10 560 and a new 1 : 10 000 Ordnance Survey map. According to Sullivan, the spores came from the more westerly of the two quarries, which must have shown a strike section along the Edgehills Sandstone. The position from where the macroflora was collected is marked on the map by a spot, and can be seen to be almost exactly along strike from the spore locality. The section now visible through the Edgehills Sandstone is summarized in Fig. 16, p. 242 (measured by the present author in 1983), and provides a striking similarity to the section as measured by Sullivan. The only noticeable discrepancy is the absence of the mudstone from immediately below the coal in Sullivan's section. However, it is characteristic of the Lower Carboniferous of the Forest of Dean for the mudstones to be lenticular, and so it is not surprising to find this one absent in the more northerly outcrop. In my view, all the field evidence points to the macro- and microflora having originated from the same interval of strata.

The macroflora was found in the bed of *c.* 70 cm of pale purple-grey mudstone immediately below the Edgehills Coal. The fossils are preserved as impressions, sometimes with a thin covering of sooty coal which is easily brushed off. Both the lithology of the matrix and the preservation of the fossils bear a striking resemblance to that seen in the classic Drybrook Sandstone flora found at Puddlebrook Quarry (Lele & Walton 1962).

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Fig. 1 Edgehills Quarry, during excavations made in 1971. Plant bed marked by arrow.

All the specimens collected by the author from Edgehills have been presented to the British Museum (Natural History) palaeobotany section. The figured material has register numbers in the range V.61742–56.

Systematic descriptions

Division SPHENOPHYTA

Order EQUISETALES

Form-genus *ARCHAEOCALAMITES* Stur, 1875

Archaeocalamites radiatus (Brongniart) Stur
Figs 4–10

1820 (?) *Calamites scrobiculatus* Schlotheim: 402; pl. 20, fig. 4.
1828 *Calamites radiatus* Brongniart: 122; pl. 26, figs 1–2.
1862 *Calamites* (*Asterocalamites*) *radiatus* Brongniart; Schimper: 321; pl. 1.
1875 *Archaeocalamites radiatus* (Brongniart) Stur: 2; pl. 1, figs 3–8; pls 2–4; pl. 5, figs 1–2.
1879 *Asterocalamites scrobiculatus* (Schlotheim) Zeiller: 17; pl. 159, fig. 2.
1964 *Archaeocalamites radiatus* (Brongniart); Crookall: 611; pl. 110, figs 1–4 (q.v. for synonymy).

DESCRIPTION. Numerous fragments of pith cast were found, which are up to 107 mm long and 32 mm wide. Only one has more than one node visible, and this has internode distances of 21 mm, 22 mm and 25 mm. More of less circular branch scars *c.* 5 mm in diameter are present on or near some nodes (Fig. 6), but no regular pattern of distribution is evident. Longitudinal

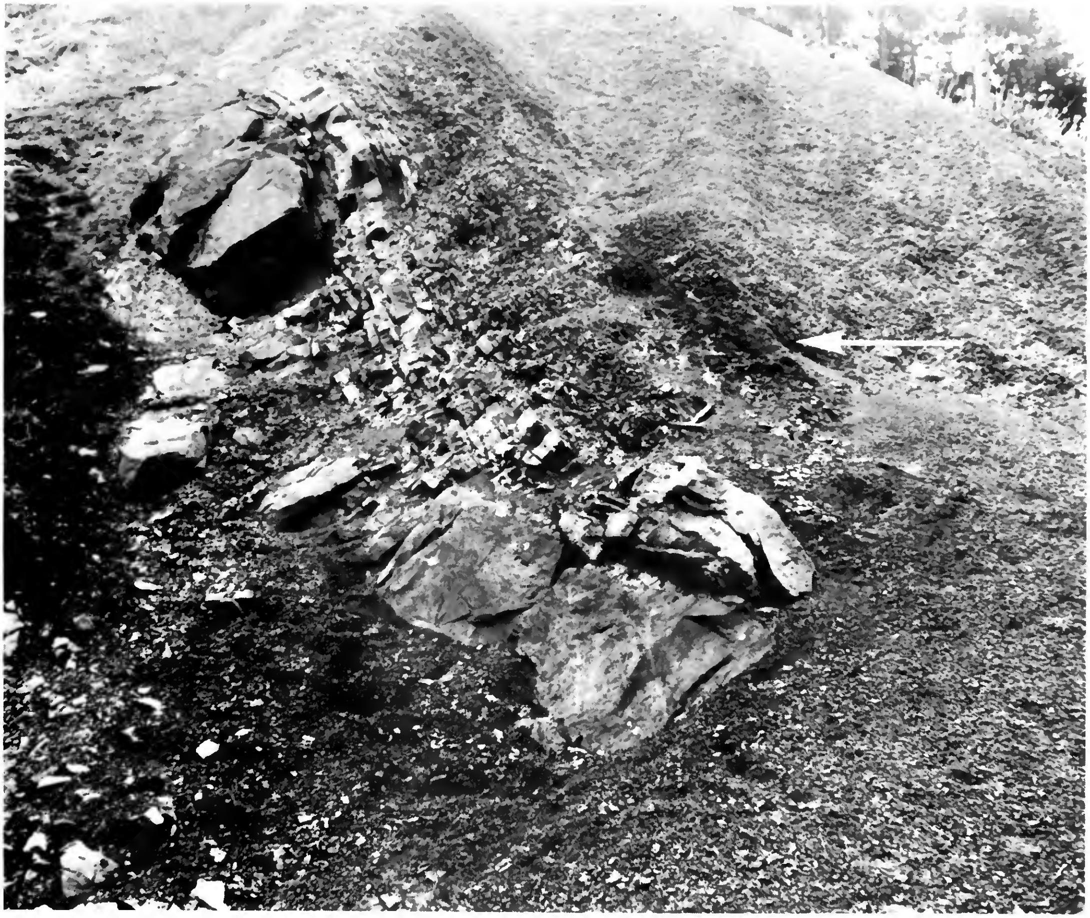


Fig. 2 Plant bed at Edgehills Quarry, marked by position of hammer. The thin Edgehills Coal (marked by arrow) can be seen just above the plant bed.

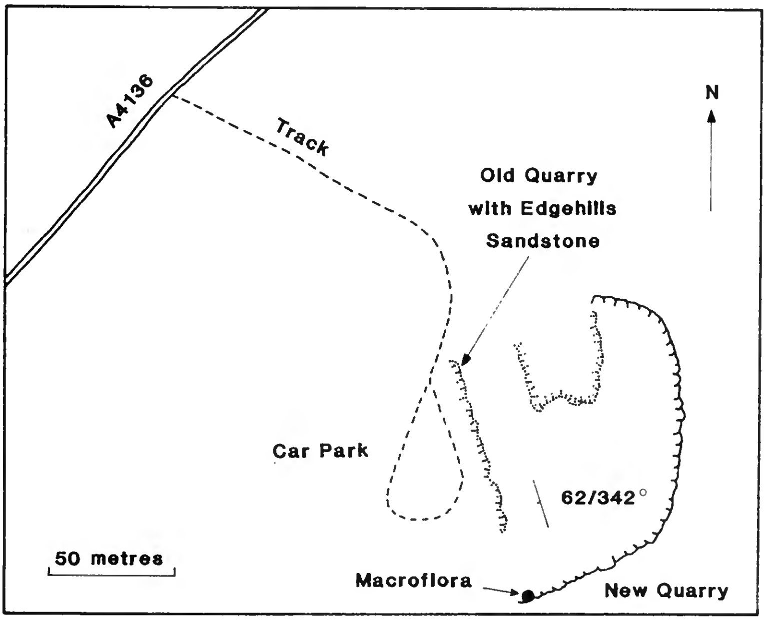
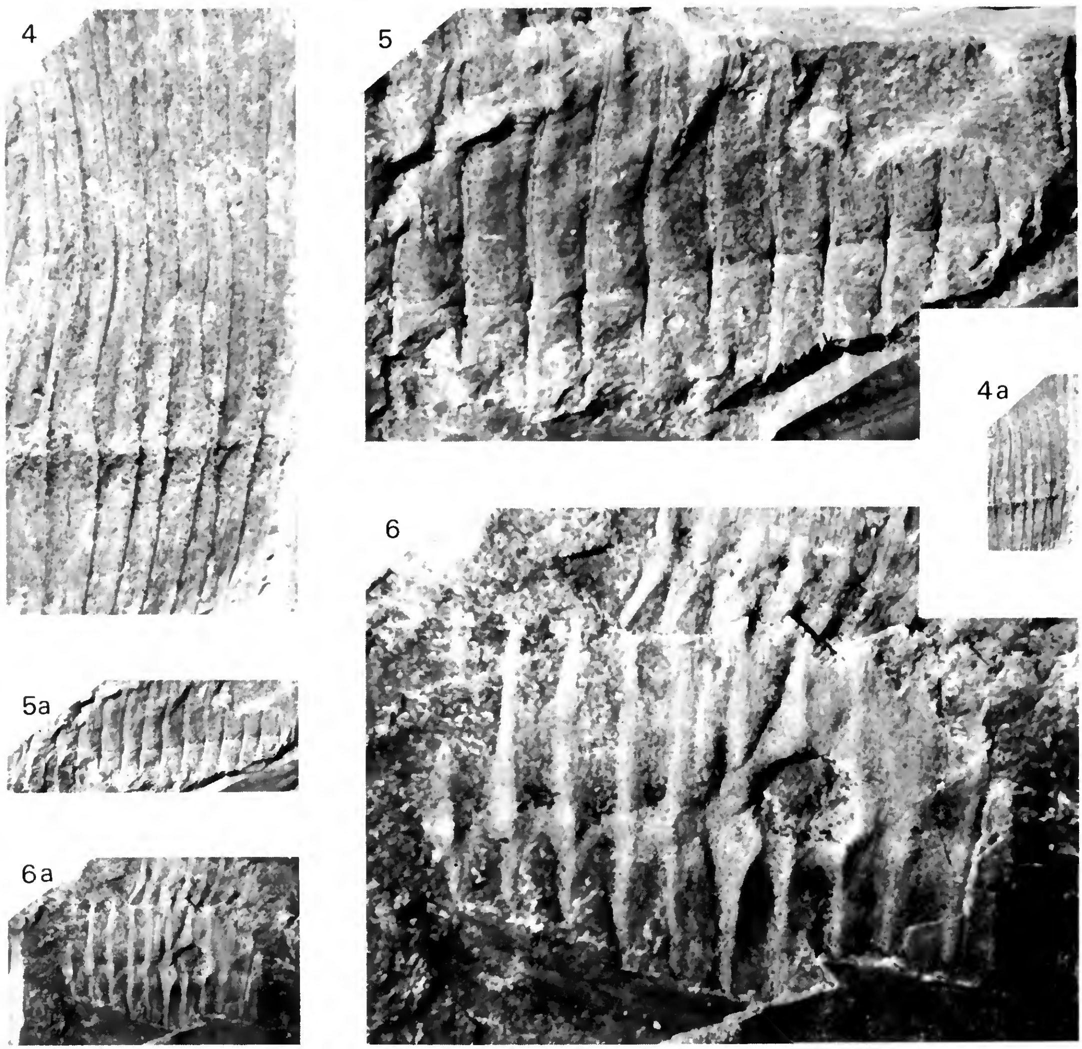


Fig. 3 Sketch map of the Edgehills area, showing positions of the old (dotted lines) and new (solid line) quarries, and the prevailing strike of the beds here. This clearly shows the relationship between Sullivan's spore locality and where the plants described in this paper were found.

ribs along the pith casts are up to 2·8 mm wide. Of the 152 ribs seen passing over a node, only 10 (6·6%) alternate (e.g. Figs 4, 7), the rest going straight over (e.g. Figs 5, 6). Two nodal diaphragms were found, both oval in shape, with average diameters of 71 mm and 34 mm (Figs 9, 10). The larger specimen shows a fine reticulation on the diaphragm, probably the impression of parenchyma cells. The diaphragm is surrounded by a stellate corona of thinner tissue, 2–3 mm wide, which is probably the splayed-out remains of the inner surface of the stem cylinder. Small oval holes occur in this tissue, *c.* 1 mm from the diaphragm. These are probably linked with leaf attachment, although no evidence of the leaves themselves was found.

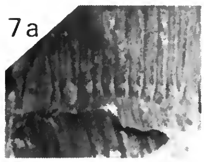
REMARKS. All the specimens of *A. radiatus* (Brongniart) found at Edgehills are fragmentary, but they clearly show the characteristic non-alternating rib pattern. Some species of *Calamites* (sect. *Mesocalamites*) have a fairly high proportion of non-alternating ribs, but never more than 90% as seen here. The nomenclatural problems surrounding this species have been discussed by



Figs 4–6 *Archaeocalamites radiatus.* Figs 4, 4a, stem showing occasional alternating ribs at node, V.61742. Figs 5, 5a, typical stem showing exclusively non-alternating ribs at node, V.61743. Figs 6, 6a, stem with branch scar at node, V.61744. Figs 4, 5, 6, × 3. Figs 4a, 5a, 6a, × 1.

7

8

7a

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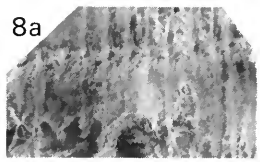


Figs 7–8 *Archaeocalamites radiatus.* Figs 7, 7a, stem showing mixture of alternating and non-alternating ribs at node, V.61745. Figs 8, 8a, larger stem showing close-up of rib–node interaction, V.61746. Figs 7, 8, × 3. Figs 7a, 8a, × 1.

Leistikow (1959), who has shown that *Archaeocalamites radiatus* (Brongniart) is the valid name, despite *Asterocalamites scrobiculatus* (Schlotheim) having been first published earlier.

There is only one previous record of *Archaeocalamites* nodal diaphragm compressions, based on specimens from Karl-Marx-Stadt in the German Democratic Republic (Hartung 1938). The German material shows no evidence of the cellular detail seen in the Edgehills specimens, although they do have attached leaves. Permineralized nodal diaphragms have been described from Loch Humphrey Burn in Scotland (Walton 1949).

Division **LYCOPHYTA**

Order **LEPIDODENDRALES**

Form-genus ***LEPIDOSTROBOPHYLLUM*** Hirmer, 1927

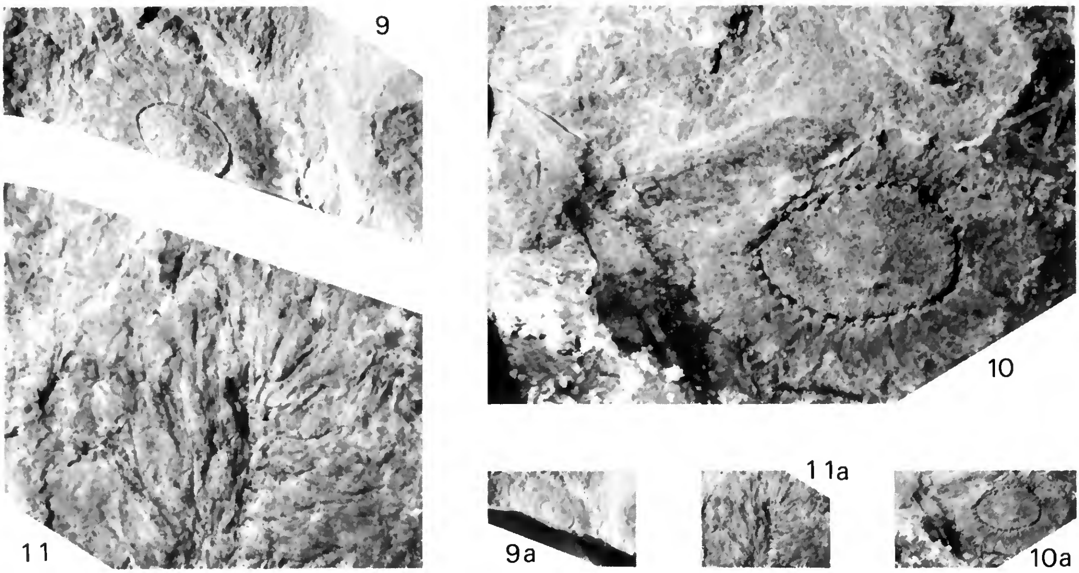
Lepidostrobophyllum lanceolatum (Lindley & Hutton) Bell

Fig. 15

1831 *Lepidophyllum lanceolatum* Lindley & Hutton: 28; pl. 7, figs 3–4.
1848 *Lepidostrobus lanceolatus* (Lindley & Hutton) Göppert *in* Bronn: 632.
1938 *Lepidostrobophyllum lanceolatum* (Lindley & Hutton) Bell: 97; pl. 98, figs 10–11.
1966 *Lepidostrobus lanceolatus* (Lindley & Hutton); Crookall: 503; pl. 99, figs 4–5 (q.v. for synonymy).

Description. Most of the specimens found were of isolated sporophylls. One part-whorl was seen (cf. Crookall 1966: pl. 99, fig. 4) but it was on a thin sliver of rock which proved impossible to extract. The sporophyll blade is 20–25 mm long and 6 mm wide. It is lanceolate with a pointed apex, and is widest $\frac{1}{2}$ to $\frac{2}{3}$ of the way along its length. A single vein *c.* 1 mm wide extends along the long axis of the blade. A fine line is often superimposed along the centre of the vein (cf. Boulter 1968: text fig. 3). The pedicle is ovoid, 4–9 mm long and 3–4 mm wide. Folds are often present along the margins of the pedicle.

Remarks. As pointed out by Crookall (1966: 506), the separation of species based on isolated sporophylls is somewhat arbitary. The Edgehills specimens are of the form known as *L.*



Figs 9–10 *Archaeocalamites radiatus*, nodal diaphragms. Figs 9, 9a, V.61747. Figs. 10, 10a, V.61748. Figs 9, 10, × 3. Figs. 9a, 10a, × 1.
Fig. 11 ?*Tomiodendron variabilis*, slender leafy shoot possibly belonging to this species, V.61752. × 3; Fig. 11a, × 1.

lanceolatum (Lindley & Hutton), which has been widely recorded from both Mississippian and Pennsylvanian floras. However, it is most unlikely that all of the recorded examples of this sporophyll-type belonged to the same natural species. The only other type of sporophyll which resembles the specimens found at Edgehills is known as *L. intermedium* (Lindley & Hutton), but this usually has a more linear blade.

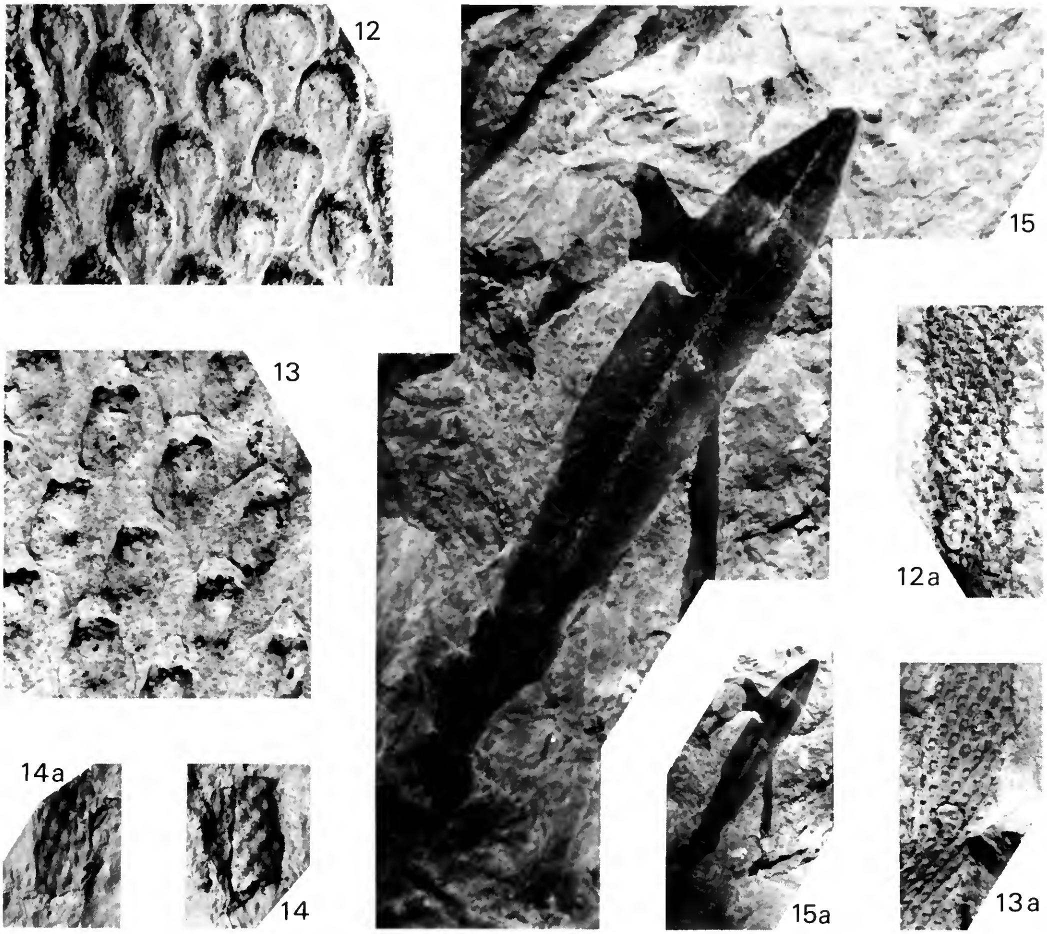
It is tempting to link these sporophylls with only the lycopod stems found at Edgehills: *Tomiodendron variabilis* (Lele & Walton); see below. However, in the only other locality to have yielded this type of stem (Puddlebrook Quarry, Forest of Dean) such lanceolate sporophylls are absent (Lele & Walton 1962). Neither have they been reported in association with other species of *Tomiodendron* (e.g. Gorelova 1978). Since the Edgehills assemblage is clearly allochthonous, any statement as to the affinities of these sporophylls based only on association would be unwise.

Form-genus *TOMIODENDRON* Radczenko 1956, emend. Meyen 1972

Tomiodendron variabilis (Lele & Walton) Thomas & Purdy
Figs 12–13, ? Figs 11, 14

1962 *Scutellocladus variabilis* Lele & Walton: 138; pl. 19, figs 1–6.
1982 *Tomiodendron variabilis* (Lele & Walton) Thomas & Purdy: 134; figs 4–14.

Description. Two specimens of stems were found showing leaf cushions, both of which are 12 mm wide. One is 35 mm long and the other 45 mm long. The leaf cushions are 3 mm long and 1·5 mm wide, and vary from oval (Fig. 13) to bulbously rhomboidal (Fig. 12) in shape. Leaves are attached to the upper part of the cushion, and appear to be persistent. Some leaf cushions have a central depression, probably owing to an infrafoliar bladder, but the preservation is too poor to be certain. The more oval leaf cushions have a small downwards-projecting protuberance, which is probably evidence of a ligule pit (Fig. 13). The leaf cushions are arranged in a steep spiral.



Figs 12–13 *Tomiodendron variabilis.* Fig. 12a, typical stem, V.61753, × 1. Fig. 12, close-up of Fig. 12a, showing rhomboidal form of leaf cushions. × 6. Fig. 13a, typical stem, but a little distorted, V.61754. × 1. Fig. 13, close-up of Fig. 13a, showing leaf cushions with more rounded shape. × 6.
Figs 14, 14a ?*Tomiodendron variabilis*, part and counterpart of decorticated stem, V.61755. × 1.
Fig. 15 *Lepidostrobophyllum lanceolatum*, isolated sporophyll, V.61756. × 3; Fig. 16a × 1.

The specimen shown in Fig. 11 shows a slender leafy stem 1·5 mm wide. It bears spirally arranged leaves, which are narrow and linear, 7–9 mm long and 1 mm wide. This is probably the distal part of a stem of *T. variabilis* (Lele & Walton).

Figs 14 and 14a are part and counterpart of a decorticated stem probably belonging to *T. variabilis* (Lele & Walton), but without evidence of the outer surface of the stem the identification cannot be confirmed.

REMARKS. Compared with the types of the species (Lele & Walton 1962), the Edgehills specimens seem to have more prominent leaf cushions. However, Thomas & Purdy (1982) have shown that this feature varies considerably in appearance in *T. variabilis* (Lele & Walton), depending on where the specimen splits, and the Edgehills specimens easily fit within this range of variation. The persistent leaves, prominent ligule pit and small infrafoliar bladder are all characteristic features of *T. variabilis* (Lele & Walton). This is only the second locality from where it has been recorded.

Division **PTERIDOSPERMOPHYTA?**

Naked axes

DESCRIPTION. Several naked axes with lateral branching occur in this flora. They are *c.* 3 mm wide. No specimen has more than one branch and so the interbranch distance is unknown. There are also larger stems *c.* 12 mm wide, with a wrinkled surface. No foliage was found attached to these stems.

REMARKS. Without foliage, it is impossible to be sure what plant-type bore these stems. However, the Viséan age indicated by the rest of the flora tends to point to pteridosperm rather than fern affinities. The larger wrinkled stems are rather similar to the 'Spindelreste von Pteridophylla' of Nathorst (1914: pl. 1, figs 3–5). Lyginopterid pteridosperm stems have comparable surface markings owing to sclerotic plates in the cortex.

Discussion

The flora consists almost entirely of equisetes and lycopods, with only rare examples of ?pteridosperm axes. It is clearly an allochthonous assemblage, the plants being fragmentary and well sorted. This sorting is well demonstrated by the proportions of the different organs found for the different group of plants.

	stems	foliage	fructifications
equisetes	a	—	—
lycopods	r	r	a
?pteridosperms	r	—	—

a = abundant r = rare — = absent

Such equisete/lycopod dominated assemblages have been referred to as 'flöznahe' (Havlena 1961), indicating that they grew in or near the coal-forming swamps. In the Westphalian, they have been reported from mudstones interpreted as prodelta lacustrine deposits (Scott 1978).

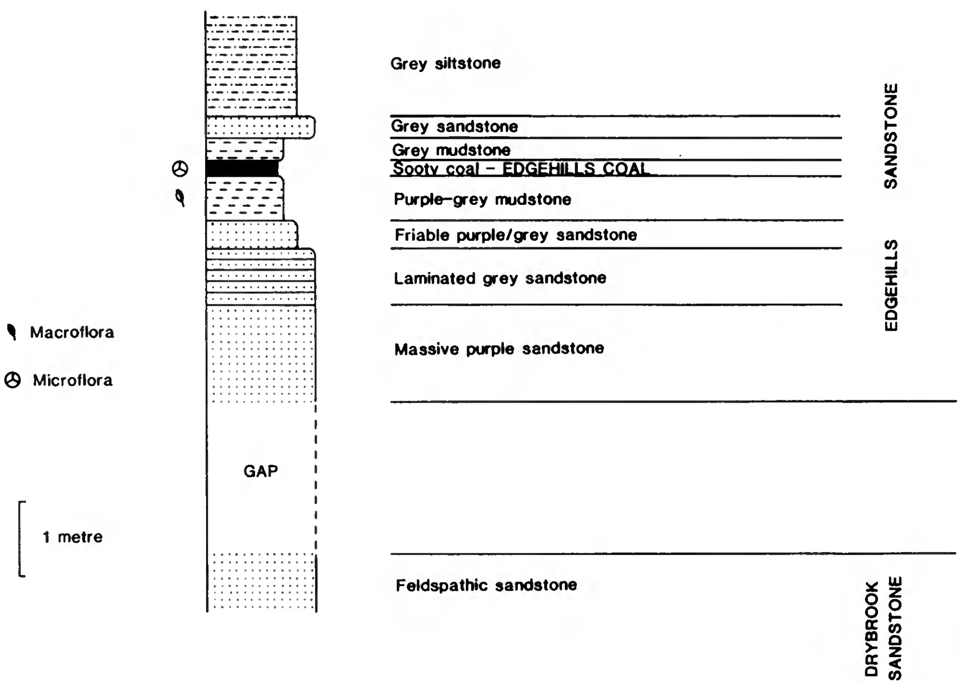


Fig. 16 Stratigraphical section through the Edgehills Sandstone, as seen in March 1983.

Under normal circumstances, such a flora would not be used for biostratigraphy. Assemblages dominated by foliage, particularly of ferns, pteridosperms and equisetes are usually preferred for such work. However, it is the only evidence available for the Edgehills Sandstone (other than the palynology) and so it is important to analyse whatever it can tell us.

Crookall (1932) stated that *Archaeocalamites radiatus* (Brongniart) occurs in the Oil Shale Group and Carboniferous Limestone 'Series' of Scotland, suggesting a stratigraphical range from about the late Asbian to the Arnsbergian. Elsewhere in western and central Europe, the most comprehensive floral records for strata of this age are from Moravia in Czechoslovakia (e.g. Hartung & Patteisky 1960, Purkyňová 1977), where *A. radiatus* (Brongniart) extends up to the Nanetta Marine Band (middle Pendleian). In the Soviet Union it is stated to have a latest occurrence in the upper Serpukhovian, below the D_4 limestone (Novik 1968, Aisenverg *et al.* 1979) which correlates with about the middle Arnsbergian. North American records show that it extends up to the top of the Mississippian (Pfefferkorn & Gillespie 1982), which is probably also equivalent to a level somewhere in the Arnsbergian (Manger & Saunders 1982). Recently, Tidwell (*in* Webster *et al.* 1984) has stated that it is known to extend up into the Westphalian A, but does not give the evidence on which this is based. Certainly all the published records suggest that *A. radiatus* (Brongniart) does not range above the Arnsbergian or its correlatives (cf. Wagner 1984: 114).

The *Lepidostrobophyllum lanceolatum* (Lindley & Hutton) type of sporophyll has a long stratigraphical range. In Britain it has been recorded from the lower Mississippian Cementstone Group (Crookall 1932) through to the Westphalian D (Dix 1934). It is thus of little biostratigraphical value.

Tomiodendron variabilis (Lele & Walton) is only known from one other locality: Puddlebrook Quarry in the Forest of Dean. Here it is found in the Drybrook Sandstone, which is probably of middle Asbian age (Sullivan 1964, George *et al.* 1976). *Tomiodendron* is principally a Mississippian form-genus (Meyen 1976, Gorelova 1978).

The macroflora clearly indicates an early Carboniferous (i.e. Mississippian) age for the Edgehills Sandstone. This agrees with the field evidence, there being no evident non-sequence between the Edgehills and Drybrook sandstones. However, it is in marked contrast to the Westphalian A age suggested by Sullivan (1964) and Spinner (1984), based on palynological evidence. Sullivan based his conclusions on an assemblage of 43 microspore form-species. Several of the species which he regarded as supporting a Westphalian A age have since been reported at much lower horizons in the Arnsbergian and Pendleian, viz. *Cirratriradites saturni* (Ibrahim), *Crassispora kosankei* (Potonié & Kremp) and *Apiculatisporis variorcorneus* Sullivan (see Owens *et al.* 1978, Owens 1982, Coquel *et al.* 1984, Owens *et al.* 1984). It is also noticeable that several of the species usually associated with lower Westphalian A microspore assemblages were not reported from the Edgehills Sandstone, in particular the group allied to *Triquitrites sinani* Artuz (Owens *et al.* 1978), and *Densosporites annulatus* (Loose) (Smith & Butterworth 1967). On the other hand, there are aspects of the assemblage described by Sullivan which support a lower Westphalian A designation, particularly the *Florinites* and *Raistrickia* components. It would seem that the evidence provided by Sullivan's assemblage is rather equivocal for assigning an age to the Edgehills Coal. In order to obtain additional palynological data, the present author collected another specimen of the coal, as well as taking examples of the mudstones immediately underlying and overlying it. E. Spinner (University of Sheffield) kindly processed this material, but only found very poorly preserved spores, in marked contrast to the abundant and beautifully preserved specimens described by Sullivan. The problem clearly requires further investigation, perhaps using fresher samples than were available during this study.

The megaspores described by Spinner (1984) from the Edgehills Coal do not clarify the issue. He found that they had the same general character to those found in the Drybrook Sandstone, and that there is no evidence of lageniculate megaspores, as would be expected in a Westphalian A assemblage. However, the dominant component, *Cystosporites varius* (Wicher), is so far unrecorded from below the Westphalian. The presence of *Triangulatisporites regalis* (Ibrahim) and *Tuberculatisporites apiculatus* (Ibrahim) also seem to support a Westphalian age,

although Spinner points out that there are a number of taxonomic difficulties with this group of megaspores.

In contrast to the above biostratigraphical evidence of the spores, the macrofloral evidence seems unequivocal. The general pattern of geological development of the area also seems to support an Asbian rather than a Westphalian A age for the Edgehills Sandstone. During the Namurian and most of the Westphalian, the Forest of Dean was part of an active area of uplift which supplied sediment to both the South Wales and Bristol/Somerset basins. Sullivan argued that there must have been a pause in this uplift during the early Westphalian A, allowing sediment to spread out eastwards from the South Wales basin. There is indeed some evidence that tectonic activity in the area was reduced during the early Westphalian A, Bluck (1961) showing that there was little coarse sediment derived from the east coming into the South Wales basin at that time. However, channel vectors determined by Bluck continue to show a predominantly westerly current flow in the eastern part of the South Wales basin. Furthermore, the isopachyte map given by Leitch *et al.* (1958) for the basal Westphalian A strata in south Wales shows a marked thinning of the sequence towards the east. Although perhaps not as dynamically active as at other times during the Carboniferous, the Forest of Dean was still an upland area during the early Westphalian A and is thus unlikely to have been the site of any major sedimentation at this time. If the existence of Westphalian A strata in the Forest of Dean were eventually proved, then they would have to be localized upland deposits, unconnected with the major basinal systems in south Wales and Avon–Somerset. However, the available evidence suggests that the Edgehills Sandstone is probably Asbian in age, and is not a relict of a period of Westphalian sedimentation in the Forest of Dean.

Acknowledgements

This paper is dedicated to the memory of Miss Morag Jones, who helped the author in the fieldwork at Edgehills Quarry, a few months before her fatal road accident in north Africa. The work is a byproduct of a survey of British Westphalian sites, carried out for the Nature Conservancy Council, Geological Conservation Review Unit, at the invitation of Dr G. P. Black. Thanks go to the staff of the unit for help with the work, especially to Mr P. Cann for library assistance. The palynological problems which arose from the study have been discussed with Dr M. A. Butterworth, Dr G. Clayton, Mr S. Jusypiw, Dr J. B. Richardson and Dr W. A. Wimbledon who are thanked for their advice. Finally, I would like to thank Dr B. A. Thomas, Dr H. J. Sullivan, Dr E. Spinner and Mr C. H. Shute for critically reading the manuscript and making numerous helpful suggestions.

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Lithogeochemical study of some Mendip country rocks with particular reference to boron

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Synopsis

This report presents quantitative data for 20 elements in 37 samples from the Mendip Hills, Somerset, England. The data were collected to attempt to identify the source of boron which contributed to the formation of B-bearing minerals in the Mendips region, and to help clarify the nature of the mineralization processes that occurred in the area.

Introduction

The Mendips ore-field (Fig. 1) has been the scene of occasional mining and quarrying activity–concerned principally with the winning of ores of Pb and Zn, and to a lesser extent, those of Mn and Fe—for about two thousand years. The major geological features of the ore-field were described by Green (1958), whilst Gough (1930) presented a comprehensive history of mining in the Mendips.

The Mendips Pb–Zn ores have been studied extensively and, in one such study, Worley & Ford (1977) compared them with other examples of carbonate-hosted Pb–Zn mineralization, particularly the Mississippi Valley type. Models describing this type of mineralization are often based on the migration of metalliferous basinal fluids (Ford 1976; Emblin 1978). However, it is probable that saline groundwaters derived from Triassic sediments were also of importance

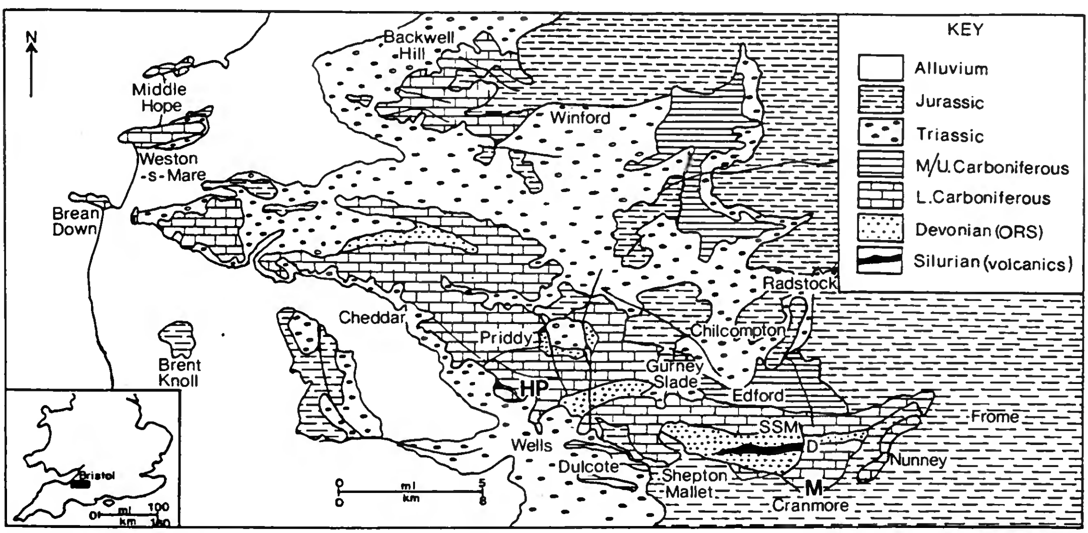

Fig. 1 Simplified geological map of the Mendip Hills, showing the principal localities represented in this study (based on the British Geological Survey 1-inch series, sheet nos 279–281 and Bristol special sheet). D = Downhead; HP = Higher Pitts; M = Merehead Quarry; SSM = Stoke St Michael.

with regard to mineralization in the Mendips, particularly in the formation of the Fe and Mn deposits. Furthermore, interaction of such fluids (or their products) might have led to the formation of the suite of secondary Pb and Cu minerals described by Spencer & Mountain (1923) and Symes & Embrey (1977) which, to date, is unique to the Mendips area.

The association of boron-bearing minerals with some areas of secondary mineralization (Symes 1977) and the paucity of data relating to the geochemical behaviour of B led us to include this element, as well as Li and Be, in the study.

To understand how the Mendips ore deposits and their secondary Pb and Cu minerals were formed, it is necessary to know the distributions and concentrations in the associated country rocks of certain trace elements which could have been the sources of enrichment of groundwaters or other fluids in the past. We have, therefore, sampled and analysed a selection of country rocks, various ore bodies and zones of secondary mineralization in the area.

Collecting strategy

A total of 37 specimens, which are briefly described in Table 1, were collected for whole-sample analysis from a variety of locations according to the following strategy.

Carboniferous Limestone

Campain (1981) presented concentration and distribution data for 15 elements (Ba, Cd, Co, Cu, F, Fe, Li, Pb, Mn, Ni, Cr, Sr, Ti, V and Zn) in Carboniferous Limestone chip samples from the Mendips region. Accordingly, our sampling of Carboniferous Limestone was largely restricted to the mineralized areas.

Shales, sandstones and zones of iron–manganese mineralization

Shales, in comparison with sandstones, limestones and evaporites, are relatively enriched in many trace elements, including Cu, Pb and Zn (Wedepohl 1969–78), which occur in the mineralized areas of the Mendips region. Consequently, it is possible that leaching of Palaeozoic shales by Triassic groundwaters could have provided metal-bearing solutions which, under suitable pH and Eh conditions, would have precipitated hydrated oxides of Mn and Fe containing Cu, Pb and Zn.

Therefore, Carboniferous shales and material characteristic of the zones of Mn and Fe mineralization were collected from the Mendips area. The distributions of trace metals in Mn–Fe pods at Merehead Quarry were studied in detail by Thorne (1975), hence many of our specimens were selected to be representative of country rocks associated with the Merehead vein 1 type of formation (see Fig. 2).

The sandstones at Gurney Slade and Stoke St Michael were sampled to complete the coverage of sedimentary rocks.

Evaporites

Rankin & Criddle (1985) have shown that low-temperature saline groundwaters derived from Rhaetic–Triassic sediments were involved in iron mineralization in south Wales. Therefore, samples from various Triassic horizons—including evaporites from the Central Somerset Basin (Whittaker 1972) and celestine-rich and siliceous nodules from Dulcote Quarry (Harding 1978)—were collected for analysis.

Mesozoic rocks

Although most of the Pb and Zn mineralization is associated with Carboniferous Limestone or Dolomitic Conglomerate, galena and sphalerite-bearing veinlets are present in younger rocks (Rhaetic to Inferior Oolite). The veinlets sometimes continue upward from the Carboniferous rocks into the younger Jurassic rocks (Alabaster 1976; Stanton 1982); consequently these Mesozoic rocks were also sampled.

Volcanic rocks

The Silurian andesites of the Beacon Hill pericline and the substantially altered Carboniferous lavas in the Weston-super-Mare area are the only volcanic rocks in the Mendips region. Since

Table 1 Material submitted to whole-sample analysis. Brief description of specimens 1–37, with locality and National Grid reference.

1. Black Rock Limestone with minor hematite veining. Carboniferous Limestone Series. Vein 1, Merehead Quarry, Cranmore, Somerset. ST 695440.
2. Clifton Down Limestone. Carboniferous Limestone Series. Adjacent to galena/baryte vein. Hobbs Quarries, Backwell Hill, Somerset. ST 504684.
3. Black Rock Limestone. Carboniferous Limestone Series. Unmineralized limestone, 4 ft from podiform manganese deposit. Vein 1, Merehead Quarry, Cranmore, Somerset. ST 695440.
4. Carboniferous Limestone with minor manganese oxide veining. Coombe Farm Quarry, Henbury, Bristol. ST 562778.
5. Silica nodule, 'potato stone'. Keuper Marl, Trias. Dulcote Quarry, near Wells, Somerset. ST 565443.
6. Andesite. Silurian. Moons Hill Quarry, Stoke Lane, Stoke St Michael, Somerset. ST 662461.
7. Dolomitic Conglomerate. Trias. Partially mineralized, *in situ* above adit into old iron mine. Higher Pitts Farm, Priddy, Somerset. ST 534492.
8. Massive gypsum. Trias. Blue Anchor, near Watchet, Somerset. ST 034436.
9. Massive anhydrite (BGS no. 908/02). Trias. Burton Row, Brent Knoll Borehole, Somerset. ST 336521.
10. Massive halite (BGS no. 700/54). Trias. Burton Row, Brent Knoll Borehole, Somerset. ST 336521.
11. Nodular bedded celestine, in Triassic matrix. Yate, Gloucestershire. ST 713835.
12. Massive hematite and goethite associated with secondary Mn/Pb/Cu mineralization. Vein 1, Merehead Quarry, Cranmore, Somerset. ST 695440.
13. Galena/baryte vein. Hobbs Quarries, Backwell Hill, Somerset. ST 504684.
14. Massive silica-rich hematite. Winford Quarry, Winford, Somerset. ST 535638.
15. Massive manganese oxides associated with secondary Pb/Cu mineralization. Vein 1, Merehead Quarry, Cranmore, Somerset. ST 695440.
16. Massive manganese oxides associated with secondary Pb/Cu mineralization. Higher Pitts Farm, Priddy, Somerset. ST 534492.
17. Limestone. Inferior Oolite. Eastern quarried segment above unconformity. Merehead Quarry, Cranmore, Somerset. ST 695440.
18. Conglomerate (Jurassic) partially overlying vein 1. Merehead Quarry, Cranmore, Somerset. ST 695440.
19. Dolomitic Conglomerate. Trias. Chilcompton Railway Cutting, Chilcompton, Somerset. ST 631512.
20. Nodular bedded celestine. Keuper Marl, Trias. Dulcote Quarry, near Wells, Somerset. ST 565443.
21. Keuper Marl associated with celestine and silica nodules. Trias. Dulcote Quarry, near Wells, Somerset. ST 565443.
22. Upper Coal Measures shale. Writhlington Tip, near Radstock, Somerset. ST 703552.
23. Black Shale. Lower Coal Series, Carboniferous. Edford, Somerset. ST 669488.
24. Lower Limestone Shales. Carboniferous. Roadside cutting near Stoke St Michael, Somerset. ST 669468.
25. Sandstone. Quartzite Sandstone Group. Millstone Grit Series. Gurney Slade, Somerset. ST 632495.
26. Sandstone. Portishead Beds. Old Red Sandstone. Stoke Lane, Stoke St Michael, Somerset. ST 662464.
27. Black Rock Limestone. Carboniferous. Murder Coombe, near Frome, Somerset. ST 743485.
28. Amygdaloidal andesite. Silurian. Downhead Quarry, Downhead, Somerset. ST 688462.
29. Massive manganese oxides. Vein 2, Merehead Quarry, Cranmore, Somerset. ST 695440.
30. White limestone. Rhaetic. Milton, near Wells, Somerset. ST 547473.
31. Copper sulphide vein in Carboniferous Limestone. Vein 1, Merehead Quarry, Cranmore, Somerset. ST 695440.
32. Massive manganese oxide. Coombe Farm Quarry, Henbury, near Bristol. ST 562778.
33. Massive goethite (off BM(NH) Min. Dept no. 1971,366). Llanharry mine, mid-Glamorgan, South Wales. ST 015808.
34. Massive hematite. Llanharry mine, mid-Glamorgan, South Wales. ST 015808.
35. Massive goethite. Higher Pitts Farm, Priddy, Somerset. ST 534492.
36. Altered basaltic lava, veined by calcite. Carboniferous. Swallow Cliff, Middle Hope, Weston-super-Mare. ST 324661.
37. Bedded impure limestone overlying vein 1, Merehead Quarry, Cranmore, Somerset. ST 695440.

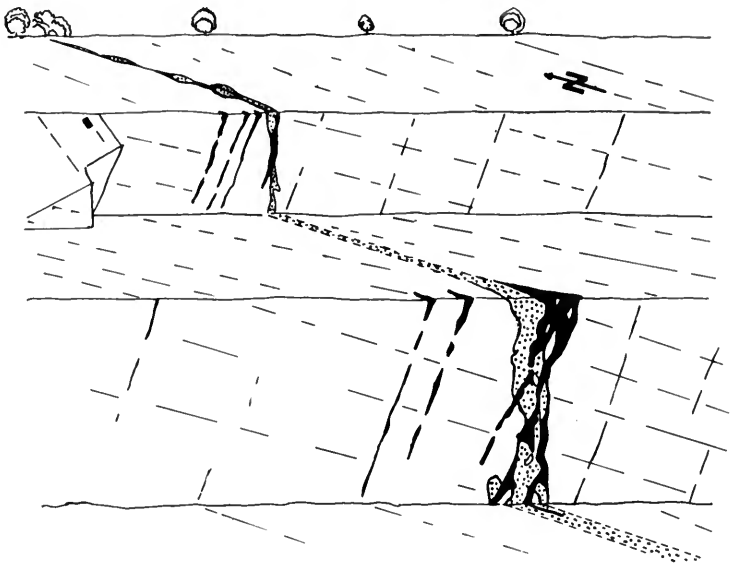

Fig. 2 Field sketch of vein 1, Merehead Quarry, after removal of thin, unconformable cover of oolitic limestone. Note the podiform nature of the vein which has a maximum width of 3·7 metres. Stipple = Mn mineralization; solid shading = Fe mineralization.

volcanic rocks are a possible source of trace-metal enrichment, representative samples of the Mendips volcanics were collected. However, the Cu minerals in the Silurian andesites at Moons Hill Quarry are probably of post-magmatic origin (Van De Kamp 1969).

Merehead Quarry

In addition to the samples described above, some Mendip mineral assemblages known to contain B-bearing minerals were selected for quantitative B distribution-mapping in order to clarify their relationships with their matrices and to attempt to determine their genesis. Merehead Quarry provides a suitable source of such samples and of material characteristic of zones of Fe and Mn mineralization in the Mendips area.

A representation of vein 1, Merehead Quarry (Symes & Embrey 1977) is shown in Fig. 2. Sampling positions were selected in an attempt to establish patterns of major and trace element contents of the host rocks associated with zones of primary and secondary mineralization in the vein. Some sections of the vein are partially filled by a quartz pebble conglomerate of Jurassic age (as shown by the fossil content) and a friable, leached and partially bedded sediment.

Techniques

Chemical analysis

The wide range of compositions of the specimens selected for whole-sample analysis, and the anticipated concentration ranges of the elements to be measured, presented a problem in analytical methodology. There are available several different analytical methods suitable for the quantitative determination of each of the 19 elements originally considered to be of potential interest. It was decided that, if possible, a single technique should be used for all the determinations, so that inter-sample data comparisons would be unaffected by errors that might otherwise be introduced by the use of different preparative and analytical procedures for a given element in different samples.

The relatively new multi-element technique of inductively-coupled plasma emission spectrometry (ICPES) was selected as the most suitable method because it is capable of measuring a

large number of elements—including many, such as B, that are difficult to measure using other techniques—over concentration ranges of several orders of magnitude (Thomson & Walsh 1983).

Because ICPES is essentially a solution analysis technique, it was necessary to find a dissolution procedure effective for all the sample types. The method devised (Din 1984) required successive fusions with potassium dihydrogen orthophosphate and potassium hydroxide. Aqueous extraction of the fusion product yielded a solution which, after acidification, was especially suitable for the determination of B because it was Fe-free. The separation of Fe from B is desirable since spectral interference by Fe with B could require the application of unacceptably large correction factors to the apparent B concentrations measured in Fe-rich solutions. Because some elements are variably distributed between the aqueous extract and the insoluble residue when this procedure is used, to determine the 19 selected elements completely it was necessary to dissolve the residue in dilute nitric acid and analyse this as well as the aqueous extract solutions.

After the ICPES analyses, the Mo content of eight specimens was determined colorimetrically by the method described by Sandell (1959) in an attempt to find areas of enrichment and possible sources of this element, an essential constituent of wulfenite which is sparingly disseminated throughout the Mendips region.

All samples were crushed and ground in agate to $<150\,\mu m$ particle size, then dried at 105°–110°C for two hours before being weighed for analysis. The ICPES analyses were made using a Jarrell-Ash Mark III Atom Comp or a Philips PV8210 spectrometer; both instruments were operated at optimum settings for simultaneous multi-element measurements. The accuracy and precision of the method were shown to be acceptable by the analysis of standard reference materials (Din 1984).

Boron mapping

The mineral assemblages selected for B mapping were cut using a wire saw, mounted in epoxy resin, ground flat and finally polished using successively finer grades of abrasive, finishing with $6\,\mu m$ or $1\,\mu m$ diamond paste. The method of Din & Henderson (1982) was used to generate quantitative B-distribution maps of the specimens. Irradiations were carried out in the vertical thermal column facility of the Imperial College Reactor Centre. Brief descriptions of the specimens together with their measured B contents in ppm by weight are given in Table 2.

Results and discussion

The whole-sample analytical data obtained are summarized in Table 3. The concentrations are quoted in ppm (by weight) except for Al, Ca, Fe, Mg and Si—data for these 5 elements are expressed as weight per cent for concentrations up to 1%. The symbols 'MIN' and 'MAJ' represent the concentration ranges $>1\%$–$<10\%$ and $>10\%$ respectively. The data for Pb in some specimens are confined to those samples which contain >1000 ppm of the element.

The light elements: Li, Be and B

No definite correlation between the measured concentrations of these three elements was observed. Therefore, it is unlikely that fluids derived from, or associated with, granitic rocks were active in the mineralization processes.

The Li contents of the limestone specimens examined are one to three orders of magnitude lower than those reported by Campain (1981) for limestone chip samples from the Mendips region. However, our data for the element correlate with those in the *Wolfson Geochemical Atlas* compiled by the Applied Geochemistry Research Group (Webb *et al.* 1978) for stream sediments from the area. The highest concentrations of Li in the samples analysed were found in the volcanic rocks, particularly the basic volcanics of the Weston-super-Mare area, with the shale horizons showing some enrichment relative to many of the limestone and mineralized specimens. In general, Be concentrations were uniformly low, with the exception of the possibly significant amounts in specimens no. 2 and 35 (Carboniferous Limestone adjacent to baryte–galena mineralization and goethite respectively).

Table 2 Boron distribution in some mineral assemblages.

Locality	Sample No.	Description	B content (ppm)
Vein 1, Merehead	B1	Mendipite	5
	B2	Mendipite, chloroxiphite, calcite and Mn-oxides	Mn-oxides 150, others 5–10
	B3	Mendipite and chloroxiphite	5–10
	B4	Chalcosine, malachite and calcite	6–7
	B5	Cerussite, calcite and Mn-oxides	4–6
	B6	Banded Fe-oxides	Goethite 150, hematite 10
	B7	Paralaurionite with mendipite	5–10
	B8	*Mereheadite, mendipite, calcite and *parkinsonite	Mereheadite > 2000, mendipite 10–20, others < 10
	B9	Mereheadite	> 2000
	B10	Mereheadite	> 2000
Vein 2, Merehead	B11	Datolite, apophyllite, calcite and goethite	Datolite > 2000, goethite 350–400, others < 5
	B12	Mereheadite	> 500
	B13	Cerussite and calcite	5–10
	B14	Goethite–Mn-oxide contact	Mn-oxide 10, goethite 100
Merehead, unclassified	B15	Manganocalcite with goethite	Goethite 250, manganocalcite 37
	B16	Wulfenite	< 10
	B17	Mereheadite and chloroxiphite	Mereheadite > 500, chloroxiphite < 10
	B18	Mereheadite, mendipite and calcite	Mereheadite > 500, others 5–10
	B19	Mendipite	5–10
	B20	Hydrocerussite	< 5
	B21	Calcite	5–10
	B22	Cerussite	5–10
	B23	Crednerite	40–60
	B25	Blixite with mereheadite	Mereheadite > 2000, blixite 15–20
Hollybrook	B24	Gypsum and celestine	< 10
Higher Pitts	B26	Mendipite	5–10
	B27	Goethite, hematite and calcite	Goethite 150, hematite 10–20, calcite 5–10
	B28	Hematite and goethite	Goethite 200, hematite 20
	B29	Wulfenite	< 10
Llanharry, South Wales	B30	Goethite	50–100
	B31	Hematite	20
Beckermet, Cumberland	B32	Hematite	25
Nunney	B33	Hematite and goethite	Goethite 120, hematite 20

* The mineral names 'mereheadite' and 'parkinsonite' have yet to be submitted for approval by the International Mineral Association's Commission on New Minerals and Mineral Names.

Table 3 Whole-sample analytical data, samples 1–37.

No.	Concentration, ppm B	Ba	Be	Co	Cr	Cu	Li	Mn	Mo	Ni	Pb	Sc	Sr	V	Zn	Concentration, % Al	Ca	Fe	Mg	Si	No.
1	2	2600	0·8	3	14	33	36	1052		8	3800	<1	338	8	63	0·3	MAJ	MIN	0·5	0·4	1
2	17	MAJ	12	143	102	74	89	52		52	214	3	MIN	10	70	0·3	MIN	0·2	0·03	MAJ	2
3	9	204	1·0	2	25	8	4	42	<1	5	28	1	257	2	13	0·1	MAJ	0·02	0·19	0·04	3
4	19	1253	2·7	659	24	87	77	MIN		75	2185	3	73	25	633	MIN	MAJ	0·8	MIN	MIN	4
5	<1	291	0·5	13	61	46	12	194		24	13	2	752	18	31	0·5	MIN	0·3	0·31	MAJ	5
6	15	113	1·4	30	206	21	94	1729		100	<5	63	169	180	89	MIN	MIN	MIN	MIN	MAJ	6
7	8	2746	2·6	<1	56	3087	5	8500	11	9	4200	1	206	136	116	0·2	MAJ	MIN	0.16	0·7	7
8	1	9	0·6	3	8	4	6	2		3	6	2	1493	2	2	0.05	MAJ	0·04	0·10	0·3	8
9	<1	10	0·5	2	6	13	3	<1		5	12	2	1323	1	3	0·01	MAJ	0·02	0·005	0·05	9
10	28	84	0·6	5	18	16	45	111		10	14	8	23	18	28	0·7	0·4	0·8	MIN	MIN	10
11	<1	MIN	0·4	<1	5	3	6	28		5	14	427	MAJ	6	3	0·3	0.09	0·4	0·05	MIN	11
12	34	1949	5·1	2	19	406	3	MIN		13	MIN	2	341	109	137	0·02	MAJ	MAJ	0·06	0·6	12
13	<1	MAJ	0·2	21	<1	15	2	90		22	MIN	<1	MIN	1	4	0·01	0·02	0·09	<0·001	0·3	13
14	62	MIN	7·0	1	8	1	10	3000		12	6	6	2525	3	2	0·05	0·04	MAJ	<0·001	0·7	14
15	12	6900	2·5	156	42	3410	3	MAJ	35	38	MIN	1	226	145	118	0·04	MIN	MIN	0·06	0·05	15
16	17	1378	2·5	127	22	3063	2	MAJ	163	15	MIN	4	52	207	616	0·07	MIN	MIN	0·14	0·2	16
17	7	1589	1·7	7	<1	12	3	715	<1	20	<1000	6	247	21	29	0·02	MAJ	0·3	0·10	0·5	17
18	14	303	<1·5	9	21	57	15	892		16	<1000	7	217	55	80	MIN	MAJ	0·7	0·54	MAJ	18
19	4	1422	<1·5	8	17	14	8	1314		23	<1000	6	141	59	299	0·4	MAJ	0·6	MIN	MIN	19
20	<1	6251	2·0	7	<1	18	5	2153		20	<1000	8	MIN	27	11	0·05	MAJ	0·5	0·33	MIN	20
21	27	208	2·0	9	21	29	30	1905		9	<1000	8	463	80	86	MIN	MAJ	MIN	MIN	MIN	21
22	42	336	4·0	22	38	41	52	1782		42	<1000	19	95	151	115	MIN	0·5	MAJ	0·86	MAJ	22
23	39	275	3·7	22	55	33	41	1183	<1	28	<1000	14	74	112	93	MIN	0·4	MIN	0·43	MAJ	23
24	82	225	3·2	19	59	19	39	860	<1	35	<1000	13	251	105	36	MIN	MAJ	MIN	0·99	MAJ	24
25	16	113	<1·5	5	128	1	6	<1		<1	<1000	4	32	23	15	0·02	0·07	0·3	<0·001	MAJ	25
26	16	233	<1·5	3	72	7	12	226		<1	<1000	5	22	43	18	<0·01	0·1	0·9	0·19	MAJ	26
27	8	33	1·0	45	28	68	12	141		64	<1000	4	419	60	92	0·3	MAJ	0·1	0·39	MIN	27
28	11	100	4·0	64	111	60	66	1103		141	<1000	20	197	165	104	MIN	MIN	MIN	MIN	MAJ	28
29	17	MIN	5·0	458	<1	2343	10	MAJ		165	MIN	3	558	744	405	0·2	MAJ	0·7	0·15	0·3	29
30	9	50	1·0	45	40	45	13	517		66	<1000	4	464	20	16	0·7	MAJ	0·3	0·30	MIN	30
31	<1	36	0·3	41	12	MIN	5	532		85	<1000	3	141	24	180	0·05	MAJ	0·2	0·10	0·3	31
32	163	3253	3·0	625	<1	1102	17	MAJ	555	212	MAJ	3	94	285	1022	0·5	MIN	0·4	MIN	MIN	32
33	34	28	5·5	78	53	65	3	161		120	<1000	2	11	85	192	0·05	0·2	MAJ	0·05	0·7	33
34	<1	13	0·3	56	36	41	8	36		76	<1000	2	11	69	113	<0·01	0·03	MAJ	<0·001	MAJ	34
35	99	31	14	78	73	67	5	431		134	1282	2	14	176	318	0·05	0·1	MAJ	0·05	MIN	35
36	17	35	6	94	251	41	167	431		271	<1000	17	48	198	263	MIN	MIN	MIN	MIN	MAJ	36
37	<1	84	0·3	39	36	63	12	959		62	<1000	4	126	46	146	0·7	MAJ	0·7	0·17	MIN	37
Detection limit	1	1	0·1	1	1	1	1	1	1	1	5 or 1000	1	1	1	0·1	0·01	0·01	0·01	0·001	0·01	

MIN = >1 – ⩽10%   MAJ = >10%

The quantities of B found are unexceptional in terms of average values for limestones and argillaceous rocks (Harder 1974) and no other B-rich areas similar to vein 2, Merehead Quarry (Figs 3a–d), were identified. The element is not associated with the sampled primary sulphide–baryte mineralization, nor is it concentrated in the specimens analysed from the Triassic evaporite suite. Halite from the Brent Knoll Borehole was the only evaporite found to contain a measurable concentration of B.

None of the volcanic rocks (Silurian andesites and altered basic Carboniferous lavas) shows any indication of association with B-rich fluids. However, in general B concentrations are relatively higher in material from the Palaeozoic shale horizons and there is a definite association of B with the goethite of banded Fe oxide mineralization (specimens no. 12, 33 and 35; see also Figs 3a–d) and particularly with the Mn oxide minerals of Coombe Farm Quarry (no. 32).

The B distribution maps (Figs 3a–d) of mineral assemblages from B-bearing zones at Merehead Quarry illustrate graphically the heterogeneity of the distribution of B and provide petrogenetic information on the assemblages. In particular, the B-rich mineral datolite has replaced B-poor baryte (areas I and II, Fig. 3b) and formed large euhedral crystals (areas III and IV, Fig. 3b). The majority of minerals contain less than 10 ppm of B. Those minerals

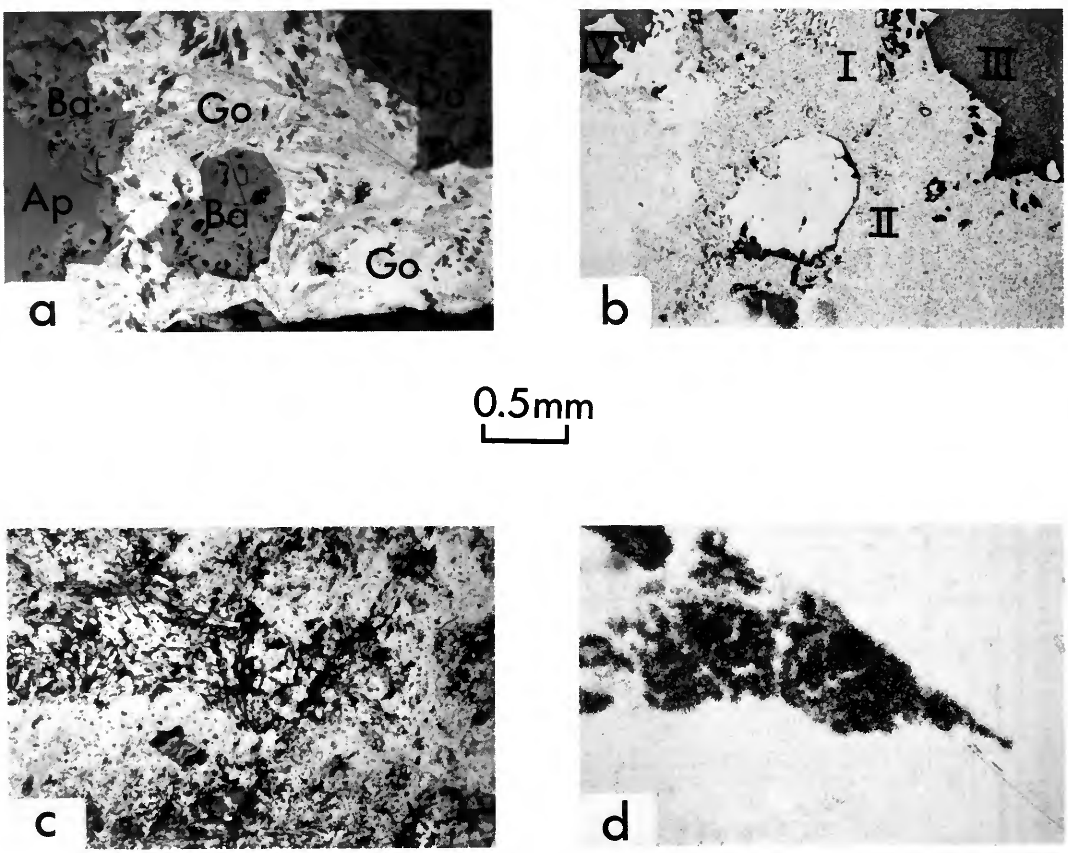

Fig. 3 a, transmitted light photomicrograph of sample B11 from vein 2, Merehead. Ap = apophyllite; Ba = baryte; Da = datolite; Go = goethite. b, B distribution map of the area shown in Fig. 3a. High track densities which correspond to high B concentrations are depicted by the darker areas. The zones marked I–IV are discussed in the text above. c, transmitted light photomicrograph of sample B12 from vein 2, Merehead (mereheadite). d, B distribution map of sample B12. The high track densities reflect the high concentration of B in mereheadite relative to the matrix.

containing more than 10 ppm of the element include mangano-calcite (37 ppm), crednerite (40–60 ppm) and the Pb oxychloride mineral mereheadite (see Table 2), which typically contains >2000 ppm. In contrast, blixite, which is closely related chemically to mereheadite, contains only 15–20 ppm B. The only borosilicate mineral observed in the suite was datolite, which contains approximately 6% of B—too much to be measured accurately under the experimental conditions used to generate the distribution maps.

The Fe oxides goethite and hematite, often intergrown at Merehead, contain significantly different amounts of B. The Merehead goethite specimens carry 150–400 ppm of B, whereas goethite (specimen no. B30) from the Llanharry ore deposit (Gayer & Criddle 1970), which is thought to have been formed in a similar manner to the Mendips iron ores, contains only 50 ppm of the element. Conversely, B concentrations in hematite from Merehead (nos B6, B27 and B28) and from Wales (no. B31) and Cumberland (no. B32) are similar and much less than in the Mendips goethite; all fall within the range of 10–25 ppm.

The alkali earth metals: Sr and Ba

As might be expected, Sr concentrations in the gypsum and anhydrite specimens (nos 8 and 9) are amongst the highest found within the suite (excluding the celestine deposits). The silica-rich hematite from Winford (no. 14), an area in which celestine is reported, also carries a significant concentration of Sr.

The celestine nodules from the Trias (specimens no. 11 and 20) and the hematite deposits of Winford (no. 14)—where hypogene baryte veins are cut by, and themselves cut, massive Fe ores—are characterized by minor to major Ba contents, and this element is typically present at the thousands of ppm level in Mn and Fe ore deposits. Conversely, the unmineralized Carboniferous Limestones contain only a few hundred ppm of Ba.

Mo and Pb

From the limited data obtained, the highest concentrations of Mo are associated with the Mn oxide pods which, in some areas, are known to contain wulfenite (Alabaster 1978, Eastwood 1983, Kingsbury 1941, Symes & Embrey 1977). The Carboniferous Limestone at Merehead, the overlying Jurassic rocks and the Palaeozoic shales are all virtually Mo-free, but there is an indication of some enrichment in the Triassic rocks. Pb, like Mo, is associated with the Mn oxide deposits and is a significant constituent of the Mn oxides found in Merehead, Higher Pitts and Coombe Farm Quarries and of the layered Fe oxides at Merehead. This element, together with Ba, is concentrated in the Triassic Dolomitic Conglomerate from Higher Pitts, relative to unmineralized limestone. The Pb (and Ba) contents of the Carboniferous Limestone adjacent to vein 1, Merehead Quarry, are also relatively high, although hand specimens show no evidence of Pb–Ba mineralization.

The transition metals: Sc, V, Cr, Mn, Co, Ni, Cu and Zn

The Sc concentrations generally correspond with the amounts suggested by Frondel (1970*a*, *b*) as average for the appropriate sedimentary and volcanic rock types, with the exception of the andesite from Moons Hill (specimen no. 6) in which the element is enriched. The remarkably high concentration of Sc in the Triassic celestine nodule from Yate (specimen no. 11) is not matched by similar or even noticeable enrichment in the other evaporites, or the mineralized specimens in the suite. All the other transition metals, with the exception of Cr, are particularly associated with the Mn oxide deposits. In contrast, Cr, somewhat unexpectedly, is concentrated (relative to the unaltered limestones) in the sandstones from Gurney Slade and Stoke St Michael (specimens no. 25 and 26).

Concentrations of V, Cr and Ni in the volcanic rocks (Silurian andesites and Carboniferous basic lavas) and shales, although unexceptional, are high in comparison with their respective concentrations in the limestones. The vanadate mineral, vésigniéite, has been identified from vein 1, Merehead quarry (D. Lloyd, personal communication 1984) where V may have been introduced by manganiferous fluids.

Copper concentrations are high in Mn oxide pods, even where secondary Pb–Cu mineralization is not evident. However, the Cu contents of the volcanic rocks, especially the andesites

from Moons Hill and Downhead, are low, in accord with Van De Kamp's (1969) data and suggestion that the element was introduced into the Moons Hill rock assemblage during a later mineralization.

Summary and conclusions

The effects of mineralizing fluids on rocks of the Carboniferous Limestone series are confined to fissure channels (characterized by rubbly, discoloured material) and their contiguous rocks. Our very limited survey of the massive, unmineralized Carboniferous Limestones (cf. Campain 1981) shows them to be relatively free of the trace metals associated with zones of Mn–Fe or sulphide mineralization. These rocks in general neither were the source of the trace metals transported by percolating groundwaters, nor were they affected by such fluids.

From the analytical data we obtained, it cannot be adduced that groundwater leaching of Palaeozoic shales in the Mendips region gave rise to the mineralizing fluids which contained the trace elements now associated with the zones of Mn–Fe mineralization. Nevertheless, it is conceivable that the shales were a source of Mn, Fe and possibly other elements including B.

Mn mineralization is a feature of the Triassic rocks (excluding the evaporite assemblages) in the Mendip area, and most of the country rocks in the area are enriched in the element. Our analytical data reflect how Mn oxides have scavenged transition metals from the mineralizing fluids. An exception to this generalization is Cr, which is present at low concentrations in the Mn oxides. Conversely, the concentration of the element in the sandstone samples (nos 25 and 26) is greater than is usual in such rocks (Shiraki 1975).

The Jurassic conglomerate and bedded sediments above vein 1, Merehead Quarry, and the Jurassic Oolitic Limestone which was the original uncomformable cover of the vein, contain similar low concentrations of trace elements. Thus it is probable that fissue channels in the area were open to mineralization during the early Jurassic.

Like the shales, the volcanic horizons could have been the source of Mn, Fe and other elements carried by the mineralizing fluids but there is no conclusive evidence to support this hypothesis.

Of the evaporites sampled from the Triassic succession, only halite (no. 10) contains a detectable amount of B. None of the evaporites is remarkable for its trace-element content, except perhaps the nodular celestine (specimen no. 11) which contains over 400 ppm Sc.

The low concentrations of trace elements in the host rocks at Merehead confirm that the mineralizing solutions were restricted to fissue channels. Mn and Fe oxides in the veins show trace-metal enrichment characteristic of other such oxide deposits in the Mendips region, even where specific minerals associated with the enrichment cannot be identified in hand specimens.

The primary Pb and Cu sulphide mineralization in vein 1, Merehead, (Symes & Embrey 1977) was subjected to reaction with pre-Jurassic mineralizing solutions which were rich in Mn and Fe and which transported other metals such as Mo, Co, V and Cu into the area. Under suitable pH conditions and chloride ion concentration (Humphreys *et al.* 1980) a series of rare Pb–Cu oxychlorides were formed by low-temperature reaction between the mineralizing solution and chloride-rich groundwaters which were probably derived from the Triassic sediments.

The source of B, which contributed to the formation of the unique suite of Pb and Cu minerals found in vein 2, Merehead, remains unidentified. A comparatively high concentration of B in the silica-rich hematite deposits at Winford (specimen no. 14) suggests that the silicifying fluids responsible for this late-stage silicification, similar to that which occurred at Merehead (vein 2, particularly), may have been B-bearing. However, if such were the case, then the B-free silica-replaced nodules at Dulcote (specimen no. 5) were probably derived from a different source of silica.

The data presented here do not allow us to propose a genetic model for the mineralization of the Mendips area. However, it is hoped that they will be useful in constraining genetic models of the mineralization which may be postulated in the future. The specimens used for this study are housed in the collection of the Department of Mineralogy, British Museum (Natural History).

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Redescription of two specimens previously recorded as fossil teuthids (Coleoidea, Cephalopoda)

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Synopsis

The two specimens *Teudopsis brodiei* Carruthers, 1871, from the Purbeck Beds of southern England, and *Teuthis* sp. Moore, 1870, of uncertain age (?Middle Jurassic to early Cretaceous) from Queensland, Australia, are redescribed and figured. They are interpreted as the remains of an indeterminate plant, and as a possible bivalve fragment, respectively. Recognition that these specimens are not teuthids affects the recorded geographical distribution and stratigraphical range of teuthids. There are at present no genuine records of fossil teuthids from Australia. The stratigraphically youngest fossil teuthid known from Britain is *Trachyteuthis latipinnis* (Owen, 1855), of Lower Kimmeridgian age.

Introduction

The Order Teuthida Naef, 1916 includes those coleoid cephalopods having a slightly curved internal shell or gladius, and typically lacking a chambered phragmocone but having a conus ventrally at the posterior end. The gladius of Recent forms is purely conchiolinic, but the fossil forms show evidence of having been mainly aragonitic.

The order includes the Suborders Loligosepiina Jeletzky, 1965, Prototeuthina Naef, 1921 and Mesoteuthina Naef, 1921 which are known only from the fossil record; also the Suborder Oegopseina d'Orbigny, 1839 known from Tertiary and Recent records, and the Suborders Myopseina d'Orbigny, 1839 and Vampyromorphina Robson, 1929 known only from the Recent (see Jeletzky, 1966). The classification of Recent and fossil teuthids is currently under review and is not discussed here.

A number of non-cephalopod and non-teuthid specimens doubtfully or incorrectly recorded as teuthids, and of teuthids recorded as non-cephalopod taxa, have been recognized by previous authors. Several similar records, some apparently forgotten or rarely cited in the literature, remain to be corrected or reinvestigated. Two specimens in the collections of the BM(NH), London, previously recorded as teuthids, are discussed below.

Descriptions

? Indeterminate bivalve fragment

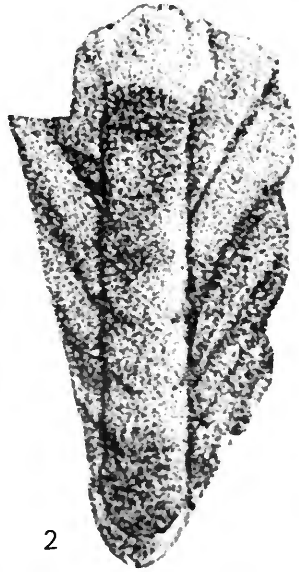
Figs 1–3

1870 ?*Teuthis* sp.; Moore: 258; pl. 16, fig. 8.
1892 ?*Teuthis* sp. indet.; Jack & Etheridge: 487; pl. 35, fig. 21.
1920 *Teuthis* sp. indet.; Bulow-Trummer: 268.
1982 ?*Teuthis* sp. (fragment of bivalve?); Phillips: 73.

DEPOSITORY. British Museum (Natural History), London. Register no. C46831.

LOCALITY. Wollumbilla, Queensland, Australia.

1



2

3

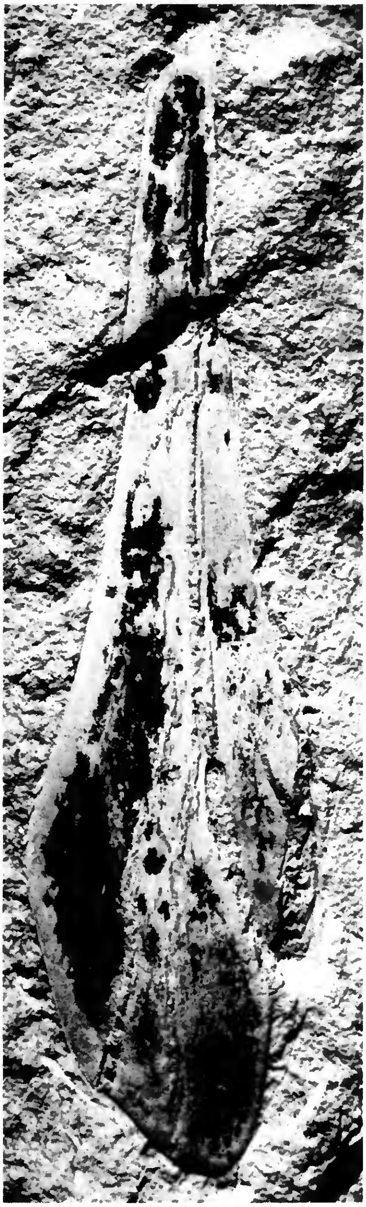
Figs 1, 2, 3 ?Bivalve fragment from Wollumbilla, Queensland, Australia (= *Teuthis* sp. of Moore, 1870). BM(NH) C46831. Fig. 1, specimen coated with ammonium chloride. × 17. Fig. 2, copy of original figure; Moore 1870: pl. 16, fig. 8. × 12. Fig. 3, scanning electron micrograph of area boxed in Fig. 1. × 55.

AGE. Uncertain. ? Middle Jurassic to early Cretaceous (see Moore, 1870: 239).

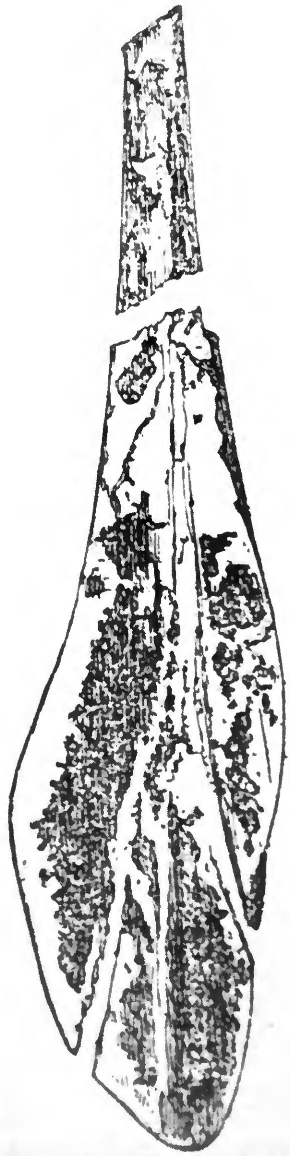
DESCRIPTION. The specimen (Fig. 1) is 6 mm in length, 3 mm wide at the broader end, and has a 'median keel' or axis 1 mm wide, about which the specimen is asymmetrical. The right side of the keeled surface shows 5 or 6 flat ribs; the left side is almost smooth, having only 2 or 3 very flat ribs. The outer margin of the right side appears complete, whereas the left outer margin and the broader end are broken. The shell consists, probably, of primary calcite, as indicated by the relatively well preserved calcite crystals (Fig. 3).

REMARKS. The specimen was originally described by Moore (1870) as a fragment of teuthid shell, and was later included in the family Loliginidae by Jack & Etheridge (1892). Bulow-Trummer (1920) mentioned it under 'Sepioidei indet.' Investigation has shown that the gladius of fossil teuthids consisted originally of aragonite and organic layers. Normally, the aragonite has been replaced by francolite, or has been dissolved completely without any replacement. The Australian specimen lacks characteristic features of a teuthid gladius in symmetry and its shell structure indicates that it is probably a fragment of bivalve shell.

4



5



Figs 4, 5 Remains of indeterminate plant from the Purbeck Beds of Dorset (= *Teudopsis brodiei* of Carruthers, 1871). BM(NH) C5251. Fig. 4, photograph of the specimen. × 2·3. Fig. 5, copy of original figure; Carruthers 1871: 448, text-fig.

Indeterminate plant
Figs 4, 5

1871 *Teudopsis brodiei* Carruthers: 448, text-fig.
1977 *Teudopsis brodiei* Carruthers; Donovan: 37.
1982 *Teudopsis brodiei* Carruthers; Phillips: 73.

Depository. British Museum (Natural History), London. Register no. C5251.

Locality. Dorset, England (exact locality unrecorded).

Age. Purbeck Beds (Upper Jurassic/Lower Cretaceous).

Description. The specimen (Fig. 4) is a lanceolate impression, 6·5 cm long and with a maximum width of 1·7 cm reducing to 0·4 cm at the anterior end (in teuthid terminology). The right half of the specimen shows a longitudinal fracture. The posterior margin is broadly rounded. The rhachis-like anterior end is incomplete. No median keel or axis of symmetry is present. Fine longitudinal striae are present on the posterior extremity. There is no evidence of a gladius-like shell. Parts of the surface are covered with a brown substance resembling lignite.

Remarks. Carruthers (1871) introduced the specific name *brodiei* for this one specimen and referred it to the teuthid genus *Teudopsis* Deslongchamps, 1835 (Family Teudopseidae van Regteren Altena, 1949; Suborder Mesoteuthina Naef, 1921). The species was subsequently ignored, but Donovan (1977) remarked on its similarity to the genus *Palaeololigo* Naef, 1921 (Family Palaeololiginidae Naef, 1921; Suborder Mesoteuthina Naef, 1921). Apart from a superficial similarity of form, the specimen shows no resemblance to a teuthid gladius, nor evidence of any typical teuthid feature. Dr C. R. Hill, Palaeobotany Section, BM(NH), to whom the specimen was shown, agrees that the specimen is the remains of an indeterminate plant.

The non-teuthid nature of *Teudopsis brodiei* Carruthers, 1871, from the U. Jurassic/L. Cretaceous Purbeck Beds, means that the youngest recorded fossil teuthid from Britain is now *Trachyteuthis latipinnis* (Owen, 1855), from the Lower Kimmeridge Clay (= L–M. Tithonian) of Dorset.

Discussion

Some incorrect teuthid references, similar to those above described, have been corrected in subsequent literature. But several doubtful records, partly indicated below, remain in need of investigation, and these may show the need to amend the present record of geographical distribution and stratigraphical range of the Order Teuthida.

Sepia vetustissima Costa, 1850 from the Aptian of Petraroia, near Naples, Italy is one of only four fossil teuthids to have been described and figured from the Lower Cretaceous (cf. Reitner & Engeser 1982). The figures of this specimen show no obvious teuthid, sepiid or even coleoid features, and it is not referred to in subsequent literature. Unfortunately the holotype appears to be lost (d'Erasmo 1914). Similarly, *Phylloteuthis incertus* Whiteaves, 1900 (correctly *P. incerta*), from the Cretaceous of the Queen Charlotte Islands, Canada, is not referred to in subsequent literature, although the paper was reviewed by Böhm (1902: 292). Dr J. A. Jeletzky (*in litt.*) has suggested, though without detailed reinvestigation, that the specimen is probably remains of an indeterminate plant.

The specimen described but not figured by Smithe (1877) as *Beloteuthis glevensis*, from the Upper Pliensbachian, *spinatum* Zone of Churchdown, Gloucestershire, England, is not mentioned in later literature and has not yet been traced. If, in fact, it belongs to *Teudopsis* Deslongchamps, 1835 (= *Beloteuthis* Münster, 1843), the first appearance of the Suborder Mesoteuthina is earlier than the Toarcian age accepted at present.

Specimens which were described as *Loligo* sp. by Lepsius (1878: 104), but not figured, were from the Upper Triassic, Rhaetian of South Tyrol. They are recorded in the faunal lists of Bittner (1889) and of Cadrobbi (1940), but not mentioned in subsequent literature. The specimens have not yet been found, neither in Darmstadt, W. Germany, nor in Strasbourg, France,

places where Lepsius was working shortly before and after his publication. Consequently, the only undoubted specimen (and species) of fossil teuthid known from the Triassic is that described by Reitner, 1978 (*Loligosepia niedernachensis*) from the Upper Triassic of the Bavarian Alps.

The doubtful status of what is now the oldest known fossil teuthid—*Glochinomorpha stifeli* from the Permian of Utah, U.S.A., described by Gordon (1971) with new specific, generic, familial and subordinal names—may be resolved by reinvestigation with the aid of scanning electron microscopy and x-ray analysis techniques.

Similarly, *Necroteuthis hungarica* Kretzoi, 1942 from the Oligocene of Budapest, Hungary—the only recorded fossil teuthid gladius from the Tertiary—requires re-examination before its suspected sepiid relationship can be confirmed (cf. *Sepia* (*Parasepia*) *orbignyana* Alvarez & Melendez, 1966 from the Miocene of Andalusia, Spain). Proof of its sepiid nature would strengthen the evidence now indicating that teuthids with calcified gladius (i.e. Prototeuthina and Mesoteuthina) died out in the Cretaceous, and only forms with an organic, non-calcified gladius, as in Recent teuthids (cf. Clarke & Fitch, 1979; Broglio Loriga & Sala Manservigi, 1975) continue beyond the Cretaceous.

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Structure and taxonomy of the Carboniferous lycopsid *Anabathra*

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Synopsis

The lepidodendralean stem, *Anabathra pulcherrima* Witham, is redescribed from permineralized material of the holotype, and its diagnosis emended. Evidence from direct comparison of xylem anatomy and from associated cortex, leaves and megasporangia indicates synonymy with permineralized stems known more commonly as *Lepidodendron brevifolium*, *L. veltheimianum* or *Paralycopodites brevifolius*, over which *A. pulcherrima* has nomenclatural priority. A stem showing both compression and permineralization modes of preservation is described. Its xylem anatomy is indistinguishable from that of *A. pulcherrima*. Its coalified leaf laminae and cuticular features compare both with *A. pulcherrima* and the compression *Ulodendron* Thomas, *non* Lindley & Hutton.

The cones originally attached to *Anabathra* stems are identified as *Flemingites*, with the rhizophore *Stigmaria* the probable rooting organ. A lectotype is selected for the cone *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas. The lepidodendralean family Flemingitaceae is emended to include the reconstructed '*Anabathra* plant'.

From the specimen described here which shows a combination of permineralization and compression/impression preservation states, it is concluded that *Ulodendron*, *sensu* Thomas 1967 (*non* Lindley & Hutton 1831) is synonymous with *Anabathra* Witham 1833. In addition to the type species, *A. pulcherrima*, the genus also includes two species previously included under *Ulodendron*, *sensu* Thomas, namely *A. thomasiana* sp. nov. and *A. landsburgii* (Kidston) comb. nov. These three species can be distinguished by their differing shapes of leaf bases and the different frequencies of stomata on them.

Introduction

Henry Witham (1830, 1831) was the first palaeontologist to describe and give illustrations of thin sections of permineralized Carboniferous plants prepared by the ground slice method. Using this technique, he examined a wide range of extant vascular plants, as well as jet, some coals, Jurassic and Tertiary woods, and certain British Carboniferous pteridosperms, coniferopsids and lycopsids (Witham 1833). Of the two lycopsid stems, *Anabathra pulcherrima* Witham has received less comment in the subsequent literature than *Lepidophloios harcourtii* (Witham) Seward & Hill. This paper aims to redescribe the neglected holotype material of *A. pulcherrima* rediscovered at the British Museum (Natural History). In the light of new observations and understanding of its structure, the diagnoses of genus and species can be emended.

By making direct anatomical comparisons, and using evidence from associated organs, it is possible to identify this type material with certain permineralized stems from other localities in Scotland, continental Europe and North America. Evidence of organic connexion or association with given genera of cones, dispersed spores and rooting organs has allowed some degree of reconstruction of the plant of which *Anabathra* represents the leafy stem. Given this model for the '*Anabathra* plant', it is interesting to see how it can be incorporated into the present classification of fossil lycopsids which are known from more or less detached organs. In particular, the familial definitions within the Lepidodendrales are in need of some revision. In part, this is a consequence of our varying knowledge of correlations between the vegetative and reproductive organs in lepidodendralean plants (Thomas 1978).

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Further problems in palaeobotany are the recognition and identification, at generic and specific levels, of given organs which have been preserved in different ways. Correlations between compressed and permineralized plants have been found within such taxa as *Sphenophyllum* (Batenburg 1982) and certain Palaeozoic Marattiales (Mosbrugger 1983, Stubblefield 1984), and some instances from the Carboniferous lycopsids are given by Chaloner & Boureau (1967). In looking for the compression equivalent of *A. pulcherrima* it is necessary to consider the relative merits of the methods available for making such comparisons. The conclusions made from these comparisons will alter the classification and naming of certain species, genera and families of fossil plants.

Historical review

The original account of *A. pulcherrima* given by Witham (1831, 1833) is discussed below in the systematic descriptions. The generic name is derived from the Greek *ἀνάβαθρον* (a seat raised on steps), because the scalariform tracheids resemble steps, and the trivial name refers to the beautifully preserved anatomy of the holotype.

There are few references to *Anabathra* in the subsequent literature, partly as a result of the retention for many years of the type material in private collections. Eleven slides of the holotype were purchased by the British Museum as part of the Nicol Collection in 1867 (Andrews 1980). The manuscript catalogue for that collection describes these slides as '*Cordaites*', '*Sigillaria pulcherrima*', or simply as 'fossil wood'. Features of the anatomy of *A. pulcherrima* given below, along with biostratigraphical considerations, leave only the last of those descriptions still appropriate. One section of the holotype obtained by Williamson (1872*a*) was purchased by the BM(NH) in 1896, nine more were transferred within the Museum from the Botany Department to the Geology Department in 1898, and the three remaining slides of this specimen were received as part of the Witham Collection in 1940. The holotype slides sent to the Museum National d'Histoire Naturelle, Paris and described by Brongniart (1839), Renault (1879, 1896), and Renault & Roche (1897) have not been traced (personal communication from Dr C. Blanc).

Lindley & Hutton (1835) and Morris (1837) closely compared the secondary xylem of *A. pulcherrima* with that of permineralized *Stigmaria ficoides*, a lepidodendralean rhizophore. However, observations made by Brongniart (1839) and King (1843–45) on the continuous cylinder of exarch primary xylem in *A. pulcherrima* distinguished it anatomically from stigmarian axes. These latter authors drew structural comparisons between *A. pulcherrima* and *Lepidophloios harcourtii* (at that time considered a species of *Lepidodendron*), and suggested the latter may represent the small branches attached in life to *A. pulcherrima*. However, there has been no subsequent evidence to support this suggestion. The production of secondary xylem in *Anabathra* was used by Brongniart to classify it, along with *Sigillaria*, *Stigmaria*, the calamites, conifers and cycads, as a gymnospermous dicotyledon. Tate (1853) also compared *Anabathra* with *Sigillaria*, but Renault (1879, 1896) distinguished the latter on its more reduced primary xylem. The primary and secondary xylem of *A. pulcherrima* led Goldenberg (1862) and Schimper (1870) to classify the species within *Diploxylon* Corda. Williamson (1872*a*) first compared the largely decorticated steles of *A. pulcherrima*, from the Viséan limestone of Pettycur in Scotland, to *Diploxylon cycadoideum* Corda. He suggested that *Anabathra* and *Diploxylon* were probably congeneric, but did not synonymize them since cortical and superficial features were lacking in the material then available to him. However, Williamson (1872*b*) later described leafy shoots from Pettycur and named them *Lepidophloios brevifolium*. In 1891, he referred this species to *Lepidodendron*, but gave no explanation for making this new combination. Moreover, the name *Lepidodendron brevifolium* had already been used for a stem compression from the Carboniferous of Czechoslovakia (Ettingshausen 1854): Williamson made no reference to these geographically and preservationally different plants, and was presumably unaware of this work of Ettingshausen.

In their account of the permineralized *Syringodendron esnostense* from the Viséan of France,

Renault & Roche (1897) drew close comparisons between that secondarily-thickened, lepidodendralean stem and *A. pulcherrima*. From examination of some holotype slides of *A. pulcherrima* then at Paris, they redescribed the secondary xylem of this species, but misinterpreted the size of the vascular rays as seen in tangential longitudinal section. They also believed the leaf traces supplied branchlets or short spines, but evidence for this is not clear from their illustration. Following Goldenburg and Schimper, Renault & Roche believed this species was very similar to *Diploxylon cycadoideum* Corda, and therefore made the new combination *Diploxylon pulcherrimum* without regard to the nomenclatural priority of *Anabathra* 1833 over *Diploxylon* 1845.

Seward (1910) named leafy shoots from Pettycur *Lepidodendron veltheimianum*, since he considered them identical to the compression/impression species *Lepidodendron veltheimii* Sternberg. Dawson had previously made this comparison, but the identification was denied by Carruthers (Williamson 1872*b*). Williamson agreed with Carruthers in that he believed there was no evidence for the association of the same form of megaspores with *L. veltheimii* compressions as those found with the permineralized *L. brevifolium* in his sense. It will be shown below that the leaf cushions bearing scars of foliar abscission in *L. veltheimii* are distinct from the leaf bases of *Anabathra*.

Although incorrect on both taxonomic and nomenclatural grounds, most permineralized *A. pulcherrima* has been described under the name *Lepidodendron brevifolium* Williamson, *non* Ettingshausen, or as *Lepidodendron veltheimii/veltheimianum* Sternberg. Scott (1911) and Long (1958) continued to recognize *Anabathra* as a separate genus of lycopsids, but did not compare the specimen from the type locality at Allanbank, Berwickshire with specimens from Pettycur, near Burntisland, Fife. DiMichele (1980) discovered that the supposedly herbaceous lycopsid *Paralycopodites minutissimum* Morey & Morey (1977) represented the lateral branchlets of a larger plant. DiMichele characterized these arborescent plants from American Upper Carboniferous coal balls using both anatomy and morphology, and identified them with *Lepidodendron brevifolium* Williamson from the Scottish Dinantian limestones. Since he demonstrated that they represented a distinct lepidodendralean genus, he placed these stems in the new combination *Paralycopodites brevifolius* (Williamson) DiMichele.

Although the type material of *A. pulcherrima* contains several megaspores, either dispersed or in megasporangia, the first intact cones associated with the species were described from Pettycur (Williamson 1872*b*). Scott (1900) named these cones *Lepidostrobus veltheimianus*, since he believed there was organic connexion in the compression state between this cone and the stem which he called *Lepidodendron veltheimianum*. However, direct evidence for this correlation is lacking. Further, the name *Lepidostrobus veltheimianus* had already been given to a different form of cone (Feistmantel 1873). Therefore, Jongmans (1930) proposed the new name *Lepidostrobus scottii* for the cones associated with leafy shoots at Pettycur. These bisporangiate cones are now generically recombined as *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas (1983). From the six syntypes referred to by Scott (1900) in his description of this species, a cone shown by Williamson (1893: fig. 52) is here selected lectotype of *F. scottii*. This specimen occurs alongside a paratype of the same species (Williamson 1893: fig. 51) in slide number V.8890 of the BM(NH) collections.

At the familial level, Goldenburg (1862) compared *Anabathra* with the Isoetaceae, while Schimper (1870) and Renault (1879) proposed affinity with the Lycopodiaceae (Jongmans 1930). These family names are now used in more restricted senses for two particular groups of herbaceous, lycopsid genera known mostly as living species. The Isoetaceae have no known pre-Permian record, although the Lycopodiaceae date from the Devonian (Chaloner & Boureau 1967). Since *A. pulcherrima* has in most descriptions been named as a species of *Lepidodendron*, its classification has varied from the family Lycopodiaceae *sensu* Brongniart 1828, to the family Lepidodendraceae of the order Lycopodiales *sensu* Potonié 1921, and following Eames (1936) to the family Lepidodendraceae of the lycopsid order Lepidodendrales (Danzé-Corsin 1962). The elevation of the lycopsids to the status of a class of vascular plants (Scott 1909) reflects our greatly increased knowledge of their diversity and peculiarity from the Silurian to the Recent, rather than unwarranted 'inflation of taxonomy' (Harris 1963).

Preservation and palaeoecology

Of the several permineralized axes Witham (1833) originally found at Allanbank, Berwickshire, he sectioned only one to describe *A. pulcherrima*. An unsectioned remnant of the holotype block of this species, V.62010, contains a decorticated stele comparing closely in size and anatomy with the ground slices described and figured by Witham (Figs 1 and 2). Witham described the matrix surrounding the stele as 'carbonaceous clay', but it contains very little fine, inorganic sediment and consists mostly of comminuted plant debris cemented by calcite. He also described the primary xylem (his 'medullary cylinder') as having been largely destroyed owing to replacement by 'siliceous matter'. However, standard mineralogical tests indicate that calcite rather than silica is the main permineralizing agent in the primary xylem, as in the rest of the block. There is no positive evidence for the presence of gypsum in the specimen, as originally described by Witham.

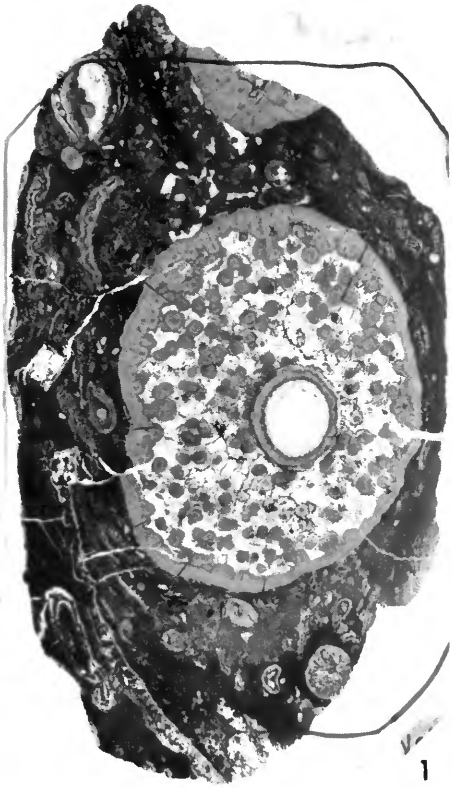
Calcite has been deposited in the holotype material in an unusual way (Witham 1833, Brongniart 1839, King 1845, Williamson 1872*b*). Spheroids of calcite, about 1·0 mm in diameter, are scattered throughout the secondary xylem, while that in the primary xylem is much more homogeneous (Fig. 3). Preservation within the spheroids is such that ornamentation of tracheid walls can be seen clearly, but in the calcite between the spheroids the cell walls are very poorly preserved or absent. There appear to be no particular nuclei for the growth of these calcitic spheroids, and the anatomy of the xylem is quite regular where preserved. This mode of calcite deposition is occasionally seen in plants from other localities in the Calciferous Sandstone Series of Scotland (e.g. Seward 1910: fig. 182). In comparable permineralized plants from the Pettycur limestone or English coal balls, the calcite has been deposited in such a way that their tissues are preserved more continuously. The Allanbank material differs from many coal balls in having less iron pyrites.

The matrix around the holotype contains no evidence of marine fossils, nor are there any remnants of rooting organs. A number of smaller axes, probably of the same species (if not the same individual) as *A. pulcherrima*, occur around the main stele. Some of these retain cortical tissues, but the larger ones tend to be partially decorticated. Several megaspores, both dispersed and in megasporangia, are also found in this matrix, but there are no intact cones. Fragments of fusinized tissue, mainly cortex, also occur here.

From these observations it appears that the limestone was deposited around this plant matter under non-marine conditions. The totally decorticated state of the larger axes indicates that they had probably been transported some distance from their site of growth, a conclusion supported by the lack of rooting organs. Although the fine organic debris may also indicate abrasion of tissues by water transport, such detritus is also typical in coal ball peats, where plant material was apparently deposited quite close to the growth position. Redox conditions reached the level required for the formation of iron pyrites (Perkins 1976). Thus, calcification probably occurred soon after deposition of the plant fragments, or there may have been enough organic matter present to generate highly anaerobic conditions during its decay. The probable source of the calcium carbonate is from dissolution of basalts, since lavas were widely extruded in Fife and Berwickshire during the Viséan (Gordon 1909).

In addition to those axes which are conspecific with *A. pulcherrima*, the matrix around the holotype also contains rachides of the lyginopteridalean pteridosperm *Lyginorachis arberi* (Long 1964) and phyllophores of the stauropteridalean fern *Stauropteris berwickensis* (Long 1966). Witham (1831, 1833) figured *L. arberi*, but he gave it no description or name. Long (1960) recorded the permineralized ovule *Genomosperma latens* from this locality and commented upon its association with *L. arberi* at other localities in the Viséan of Berwickshire. *G. latens* and *L. arberi* occur together in slide V.62016.

The outer cortical tissues of the pteridosperm rachides and fern phyllophores may have been more resistant to abrasion during transport than was the cortex of *A. pulcherrima*. However, there seems no direct means of determining whether these species lived in the same habitat. Comparable associations of pteridosperms and ferns with lycopsids in the Pettycur limestone and in many coal ball floras suggest the possibility that these three groups of plants preserved at Allanbank originated from the same community.



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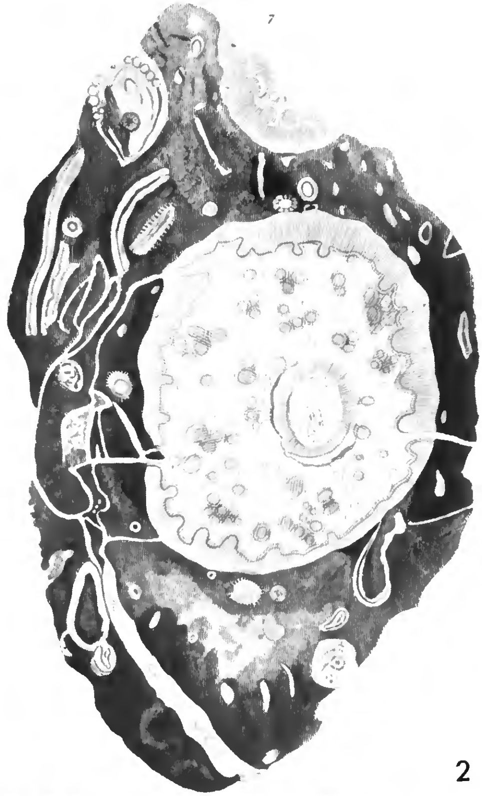

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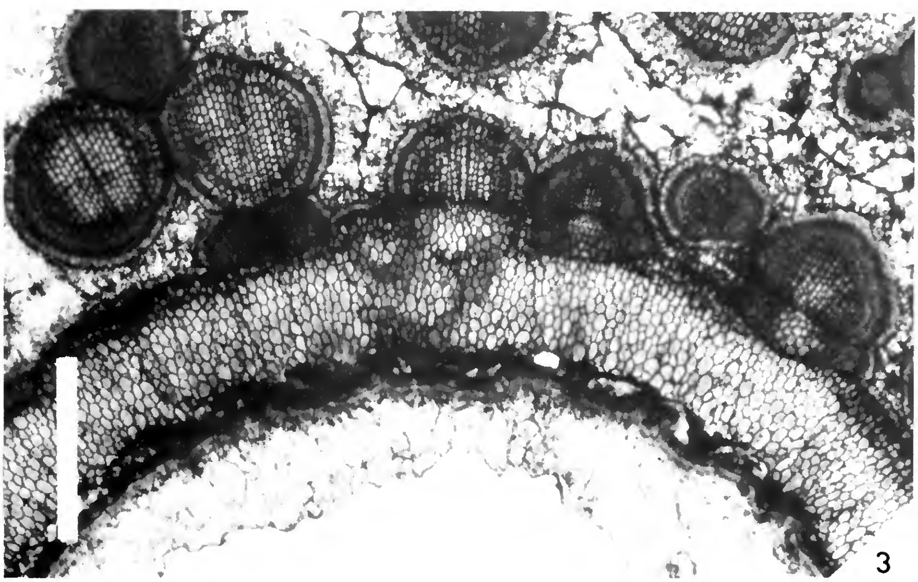

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Figs 1–3 *Anabathra pulcherrima* Witham, holotype. Viséan; Allanbank, Berwickshire. Fig. 1, complete transverse section of stele in matrix, V.62011, × 1. Fig. 2, Witham (1833): pl. 8, fig. 7. × 1. Fig. 3, detail of part of primary xylem and innermost secondary xylem in transverse section. Note the discontinuous preservation of cell walls from outer primary xylem outwards. V.62011. Scale bar represents 2·0 mm.

Systematic descriptions

Class **LYCOPSIDA** Scott, 1909

Order **LEPIDODENDRALES** Eames, 1936

Family **FLEMINGITACEAE** Thomas & Brack-Hanes, 1984, emend.

EMENDED DIAGNOSIS. Stems retaining leaf laminae throughout growth, consequently lacking foliar scars. Bisporangiate cones produced, releasing free megaspores and microspores. More than one tetrad produced per megasporangium.

TYPE GENUS. *Flemingites* Carruthers, 1865, emend. Brack-Hanes & Thomas, 1983.

Genus *ANABATHRA* Witham, 1833, emend.

1967 *Ulodendron* Lindley & Hutton, *sensu* Thomas: 778 (this generic usage is different from that of Lindley & Hutton).
1977 *Paralycopodites* Morey & Morey: 67.
1980 *Paralycopodites* Morey & Morey, emend. DiMichele: 1467.

EMENDED DIAGNOSIS. Stems with single, exarch protostele, protoxylem uniformly distributed at margin, medullated except at most distal levels. Lateral branchlets formed without associated gap in protostele of main stem. Outer primary cortex homogeneous, composed of thick-walled, longitudinally elongate cells. Outer secondary cortex (periderm) homogeneous, retaining distinct leaf traces. Stem surface bearing straight, linear leaves, spirally arranged in evident parastichies; leaf laminae retained following secondary growth of xylem and cortex in stem. Leaf bases with stomata.

TYPE SPECIES. *A. pulcherrima* Witham 1833, emend.

Anabathra pulcherrima Witham 1833, emend.

1831 'Fossil plant found at Allenbank'; Witham: pl. VI, fig. 7 (t.s. of part of secondary xylem.)
1833 *Anabathra pulcherrima* Witham: 39–42; pl. VIII, figs 7–12; pl. XVI, fig. 7.
1850 *Stigmaria anabathra* Corda; Unger: 227–228. (Unger's material differs from the type material described under this name by Corda).
1862 *Diploxylon anabathra* Goldenberg: 24.
1869 *Ulodendron minus* Lindley & Hutton; Carruthers: 227; pl. XXXI, figs 1–4. (This specimen differs in structure from the type material of *U. minus* L. & H.).
1872*a* *Diploxylon*; Williamson: 240.
1872*b* *Lepidophloios brevifolium* Williamson: 310; pl. XLIII, figs 20–2.
1886 *Lepidodendron selaginoides* Sternberg; Felix: 32–35; pl. II, fig. 3. (Misidentified leaf from German coal ball.)
1891 '*Lepidodendron brevifolium* Burntisland Form' Williamson: 58. (A homonym of a different species of Ettingshausen, 1854).
1897 '*Diploxylon pulcherrimum* de Witham'; Renault & Roche: 15–16; pl. VIII, fig. 5.
1910 *Lepidodendron veltheimianum* Sternberg; Seward: 177; text-figs 186A, B. (Comparison with the stem compression *Lepidodendron veltheimii* Sternberg).
1977 *Paralycopodites minutissimum* Morey & Morey: 64–69; pl. 1, figs 1–10; pl. 2, figs 11–19.
1980 *Paralycopodites brevifolius* (Williamson) DiMichele: 1467; figs 1–16.

EMENDED DIAGNOSIS. Leaf bases greater in length than breadth. About 350–400 stomata/mm^2 on leaf bases.

HOLOTYPE. Hand specimen, V.62010, and slides prepared from this, V.62011–33.

LOCALITY AND HORIZON. Allanbank, near Allanton, Berwickshire, Scotland. National Grid Reference: NT 864545. ('Allen-Bank' of Witham 1831, 1833; see Long 1958 for details of this site). This part of the Cementstone Group of the Calciferous Sandstone Series has been assigned a Viséan 1 or uppermost Tournaisian age within the Lower Carboniferous (Dinantian) on the basis of palynology (Meyer-Berthaud 1984).

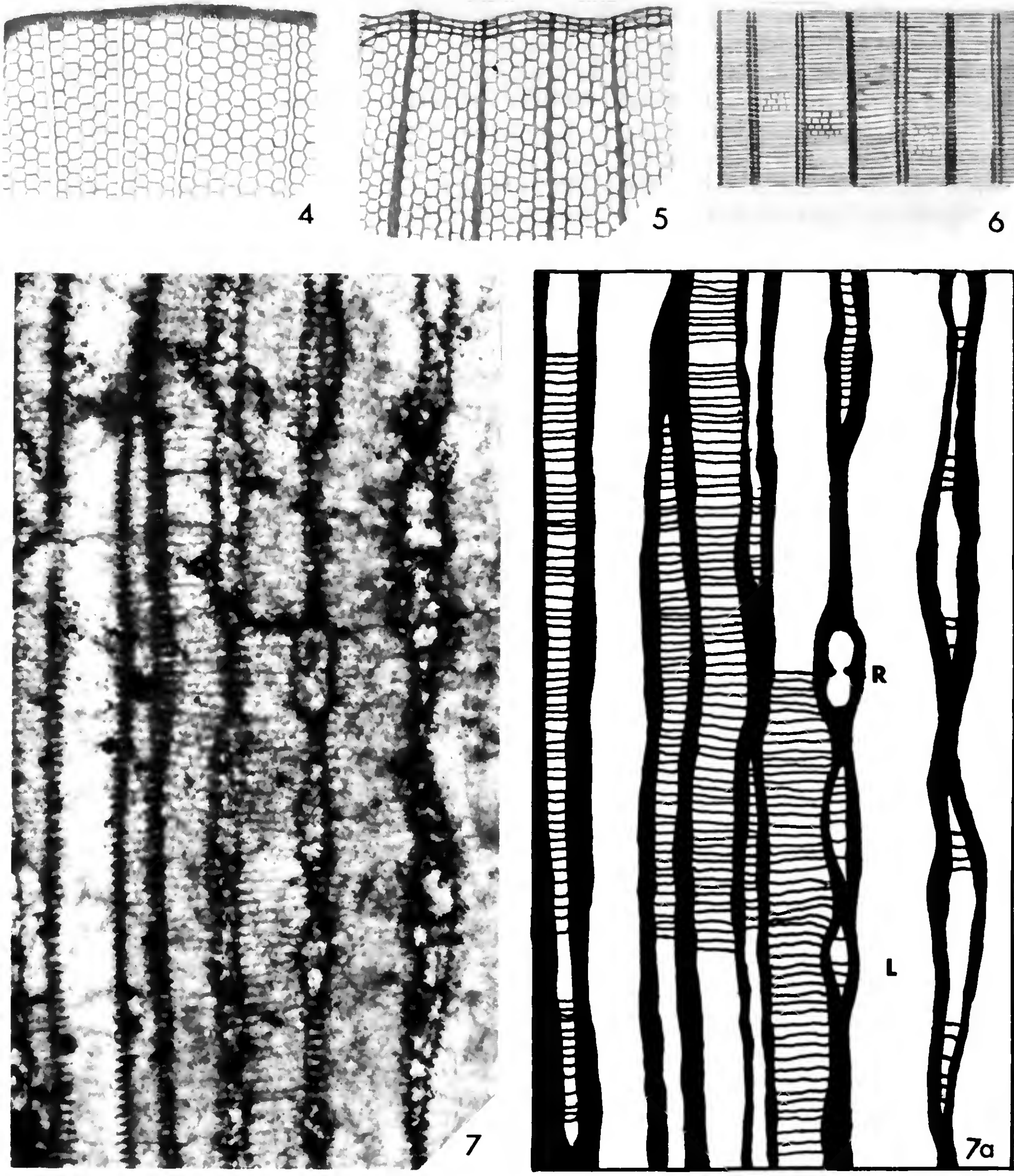
DESCRIPTION OF HOLOTYPE. Although Witham first illustrated part of the xylem of *A. pulcherrima* in 1831, he gave neither a detailed description nor the name until 1833. The original block from which a number of ground slices were prepared contained the stele of *A. pulcherrima* in the form of a truncated cone. Although Witham stated that the axis was laterally compressed, the generally undistorted preservation of the xylem indicates that the stele may have originated from part of the crown where dichotomous branching gave rise to oval rather than terete steles as seen in transverse section. The apex of the truncated cone was rounded, and measured about two-thirds of the basal diameter, but Witham gave no absolute dimensions for the unsectioned axis. Since the remaining block, V.62010, matches the larger sections prepared from the original in the size and position of the holotype axis, it presumably represents the base, with an overall diameter of about 70 mm. Witham described transverse features, at intervals of about 50 mm, interrupting the longitudinal striations seen on the surface of the axis. None of these transverse markings are visible in the remaining block, nor in the longitudinal sections prepared from the original. I agree with Witham that they do not represent constrictions or expansions in the preserved tissue, as seen in many sphenopsids, but are simply fractures passing through both fossil and matrix. Such disruptions can be seen in some of the transverse sections (Figs 1 and 2).

At the centre of the holotype axis there is a mass of apparently homogeneous calcite, between 8 mm and 10 mm in diameter, usually with a central space or gap (Fig. 3). This calcite is surrounded by a cylinder of primary xylem. It is uncertain whether the metaxylem tracheids formed continuous tissue to the centre of the stele in the life of the plant, composing a solid protostele as, for example, in *Lepidodendron rhodumnense.* Instead, there may have been a wholly parenchymatous medulla encircled by primary xylem (as in *Lepidophloios harcourtii*), or possibly there was a 'mixed pith' of tracheids dispersed amongst parenchymatous cells (as in *Diaphorodendron vasculare*). If there existed a solid protostele, it is difficult to explain why none of the inner tracheids have been preserved, given that the same block includes xylem with very well preserved tracheids. Similarly, with a 'mixed pith' one would expect to find a few tracheids preserved in this part of the stele. With a medullated protostele, however, it is much more likely that the parenchymatous tissue would have collapsed or been degraded during sedimentation, or broken down while the plant was still alive. (Williamson, 1872*a*, and DiMichele, 1980, have described other specimens of *A. pulcherrima* which have a well-preserved, entirely parenchymatous medulla.)

Witham gave no description of the primary xylem, even though in the holotype this is as well preserved as the secondary xylem. In describing his 'central medullary cylinder', Witham's figures of radial files of thick-walled cells showing hexagonal transverse sections are clearly part of the secondary xylem (Fig. 4). Primary xylem forms a continuous ring within the secondary xylem, up to 2·2 mm in radial thickness (Figs 1 and 3). Metaxylem tracheids are polygonal in transverse section, up to 360 μm in diameter and at least 540 μm in length, although no distinct end walls were encountered. As King (1845) commented, the flexuous shape of these tracheids means they exceed the length apparent in any one longitudinal section. The metaxylem tracheids show scalariform thickenings on all their walls, the transverse bars being about 6 μm apart; these bars sometimes anastomose, and in places are joined by minute fimbrils. The fimbrils, considered by some authors as diagnostic for the Lepidodendrales, but certainly unknown outside the Lycopsida, were figured by Witham from the secondary xylem tracheids (Fig. 6), although I have not observed them in the available holotype sections. Protoxylem tracheids are distributed more or less evenly in a continuous zone around the outer margin of this exarch protostele (Figs 3 and 8). They are about 30 μm in diameter, but the form of wall thickening is not clear in this material.

Secondary xylem immediately surrounds the primary xylem, reaching a maximum radial thickness of 23 mm in this specimen. There is no indication of growth rings. Tracheids quadrilateral or hexagonal in transverse section and up to 155 μm in diameter (Figs 3–5, 8) occur. Their longitudinal walls show essentially the same form of scalariform thickening as in the metaxylem. No distinct end walls are visible for secondary xylem tracheids, but many incomplete lumina between 5 mm and 10 mm in length were measured.

Vascular rays can be seen crossing the secondary xylem in tangential longitudinal section



Figs 4–7a *Anabathra pulcherrima* Witham, holotype. Figs 4–6, Witham (1833): pl. 8, figs 8, 9 & 10 respectively; all × 100. (These figures cannot be assigned to any particular slide of the holotype material.) Figs 4 & 5, secondary xylem in transverse section. Fig. 6, secondary xylem tracheids in tangential longitudinal section. Fig. 7, tangential longitudinal section of secondary xylem, V.62017. × 105. Fig. 7a, interpretive drawing of Fig. 7, showing apparent vascular ray to left of **R**, as distinct from sections of undulating tracheid walls where lumina of tracheids are partly obscured by scalariform bars, as immediately to left and right of **L**.

(Figs 7, 7a). The generally undistorted form of the stele makes it unlikely that these rays are only intercellular disruptions as suggested by Witham. They are up to 90 μm wide, and appear to be between 100 μm and 160 μm in height. Little cellular material remains in the vascular rays, but in some areas fragments of cell walls remain (Fig. 7). The longitudinal walls of the secondary xylem tracheids often undulate, repeatedly passing in and out of the plane of section.

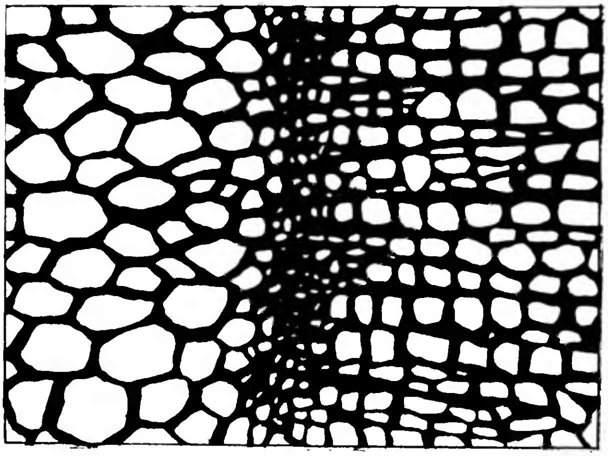


Fig. 8 *Anabathra pulcherrima* Witham, holotype. Detail of part of junction between primary xylem and secondary xylem as seen in transverse section. Note the smallest diameter tracheids, the protoxylem, arranged continuously between the large, irregularly positioned metaxylem tracheids and the radially arranged secondary xylem tracheids. V.62011, × 28.

In some places, this may give rise to apparently taller vascular rays. However, the presence of at least a few transverse bars crossing these 'rays' shows that they are only incomplete sections of the lumina of adjacent tracheids (Fig. 7a).

In a tangential longitudinal section of the secondary xylem, Witham figured a leaf trace (Figs 9 and 10). These traces, which Witham referred to as 'medullary rays', are up to 250 μm wide, and about 450 μm in height; poor preservation of the parenchymatous cells makes their limits indistinct. Scalariform tracheids, 20 μm to 30 μm in diameter, fill the central part of the leaf trace. Some can be seen in connexion with the protoxylem.

In one section, V.62032, there is evidence of lateral, pseudomonopodial branching of the axis. Just outside the main stele is a smaller, decorticated stele sectioned in the same plane. It consists of solid, primary xylem surrounded by secondary xylem, except on its surface adaxial with respect to the larger stele (Fig. 12). The overall crescentic shape of this smaller stele, and its position in relation to the main stele, indicate that it is probably a lateral branchlet. In none of the available sections of the holotype is there any disruption of the main axis which can be related to the formation of this or other lateral branchlets.

The width of secondary xylem compares closely with that of steles from large branches or the main trunk of arborescent lycopsids. As there are no extraxylary tissues preserved attached to the holotype stele, the total diameter of the original stem remains unknown.

In addition to the pteridosperm and fern organs mentioned above, the holotype of *A. pulcherrima* is surrounded by several other organs which show anatomical details of greater similarity to the holotype, and which are probably conspecific with it.

In Witham's original figure of the entire stele of *A. pulcherrima* there are shown at least two other decorticated steles showing xylem with the same structure as that of the holotype (Figs 1, 2). This anatomical comparison is supported also by longitudinal sections with both holotype and associated steles together (e.g. V.62022); although the quality of preservation and the number of available characters for comparison are limited, there are no structural differences visible to deny identity between these steles and the *A. pulcherrima* holotype. The matrix also contains a number of stems, about 5 mm to 15 mm in diameter, which retain varying amounts of outer primary cortex; they all contain single steles with only primary xylem. The steles are exarch, with the protoxylem arranged evenly and continuously around the metaxylem, giving a smooth outline to the stele in transverse section. In those steles greater than 1·5 mm in diameter, there is a hollow at the centre of the metaxylem, probably indicating medullation of the

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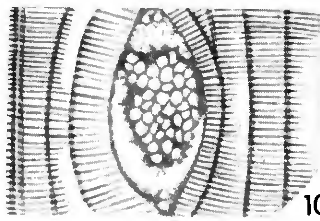
Figs 9–11 *Anabathra pulcherrima* Witham, holotype. Fig. 9, leaf trace seen in tangential longitudinal section of secondary xylem. V.62017. Scale bar represents 240 μm. Fig. 10, Witham (1833): pl. 8, fig. 12; leaf trace as seen in Fig. 9 (not assignable to any particular slide of the holotype). × 100. Fig. 11, isolated leaf lamina seen in transverse section in matrix around main stele. V.62015. Scale bar represents 1·0 mm.



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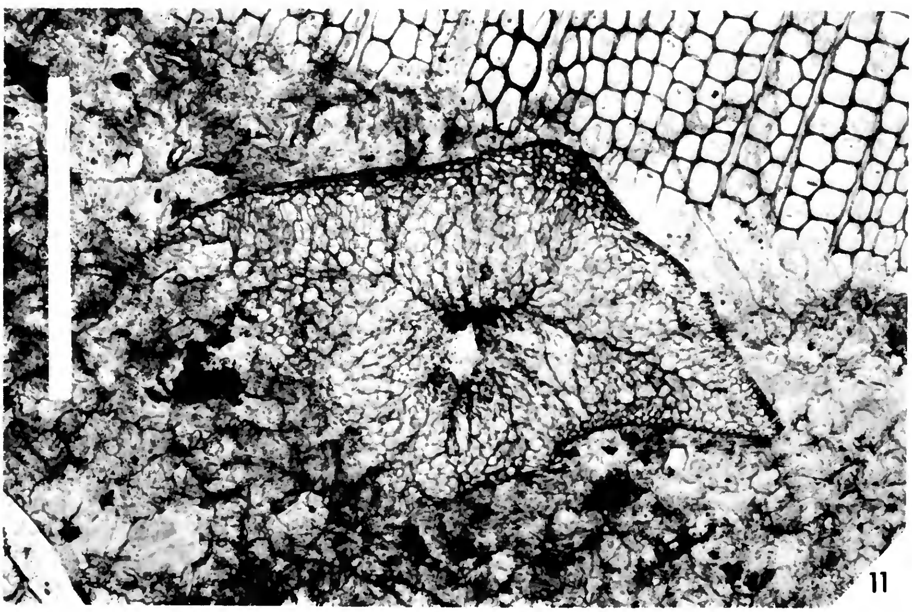

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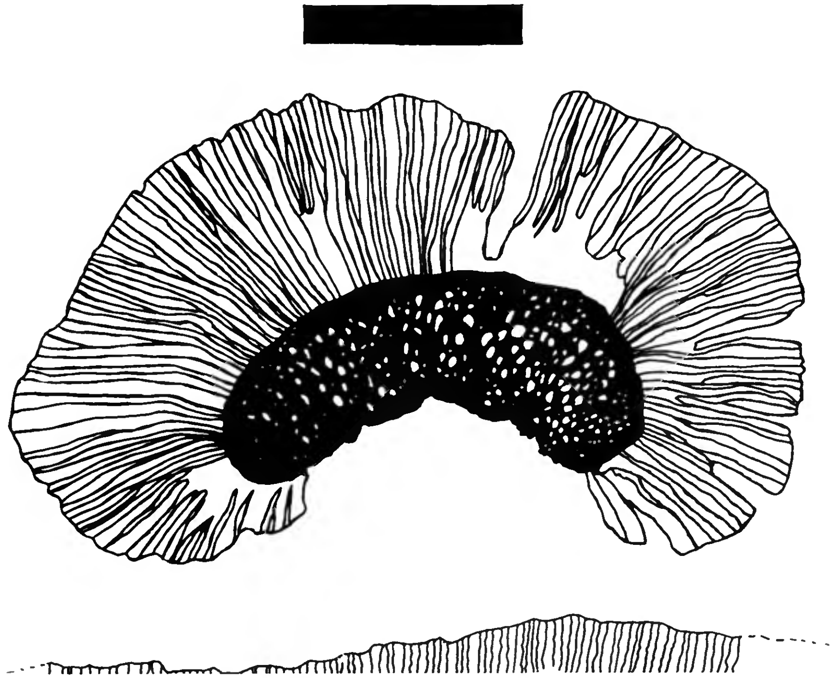


Fig. 12 *Anabathra pulcherrima* Witham. Stele of probable lateral branchlet seen in transverse section, closely associated with *A. pulcherrima* holotype. Note the eccentric, radiating files of secondary xylem tracheids surrounding the primary xylem except on its adaxial surface, opposite the scale bar. V.62032. Scale bar represents 2·0 mm.

stele. There is a gap between the protoxylem and the outer primary cortex, and the latter has often collapsed laterally around the stele. Occasionally, minute bundles of tracheids occur in this gap, probably remains of leaf traces. Outer primary cortex is preserved up to 2·5 mm wide, and is composed of a homogeneous prosenchyma of thick-walled stereids up to 90 μm in diameter and at least 450 μm long. Cortical cell diameter decreases towards the outer part of the axis, and the outermost cells appear to be shorter as seen in oblique section. In some of these stems, the cortical tissue contains rounded or oval hollows, occasionally enclosing a few obliquely sectioned, scalariform tracheids, indicating that they are leaf traces. There is no secondary growth in the cortex of these stems, and no clear leaf bases or epidermis can be seen.

Although it is difficult to compare stems with and without secondary growth, or between corticated and decorticated states, the metaxylem anatomy, arrangement of the protoxylem, and probable medullation of these smaller stems also compare so closely with the holotype stele that they are probably conspecific.

Leaf laminae, leaf bases and secondary cortex also occur in the matrix around the *A. pulcherrima* holotype. In some instances, the leaf bases are attached to secondary cortex (Fig. 13). The secondary cortex appears homogeneous across a radial thickness of 3·7 mm. The cells of this tissue are in radial files, and are rectangular in transverse section, measuring up to 20 μm radially and 36 μm tangentially. Although leaf bases and secondary cortex are in organic connexion, no leaf traces can be seen crossing the secondary cortex in the type material. In transverse section, the leaf bases appear as winged structures, extending up to about 2 mm from the outside of the secondary cortex, and about 2·5 mm in tangential width. No ligules or their pits have been found in these leaf bases. The wings of the leaf bases do not overlap tangentially. Since the leaf lamina remains attached to the stem, even after secondary growth of the cortex, it is difficult to distinguish features of the leaf base from those of the leaf lamina. The cortical cells

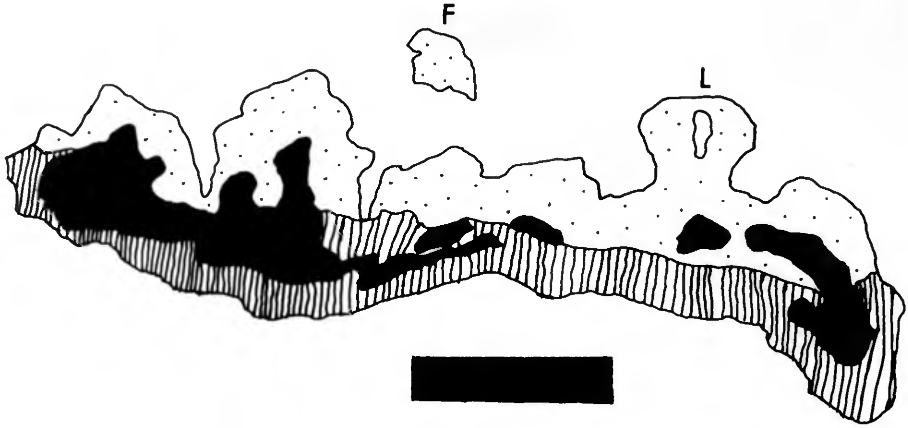
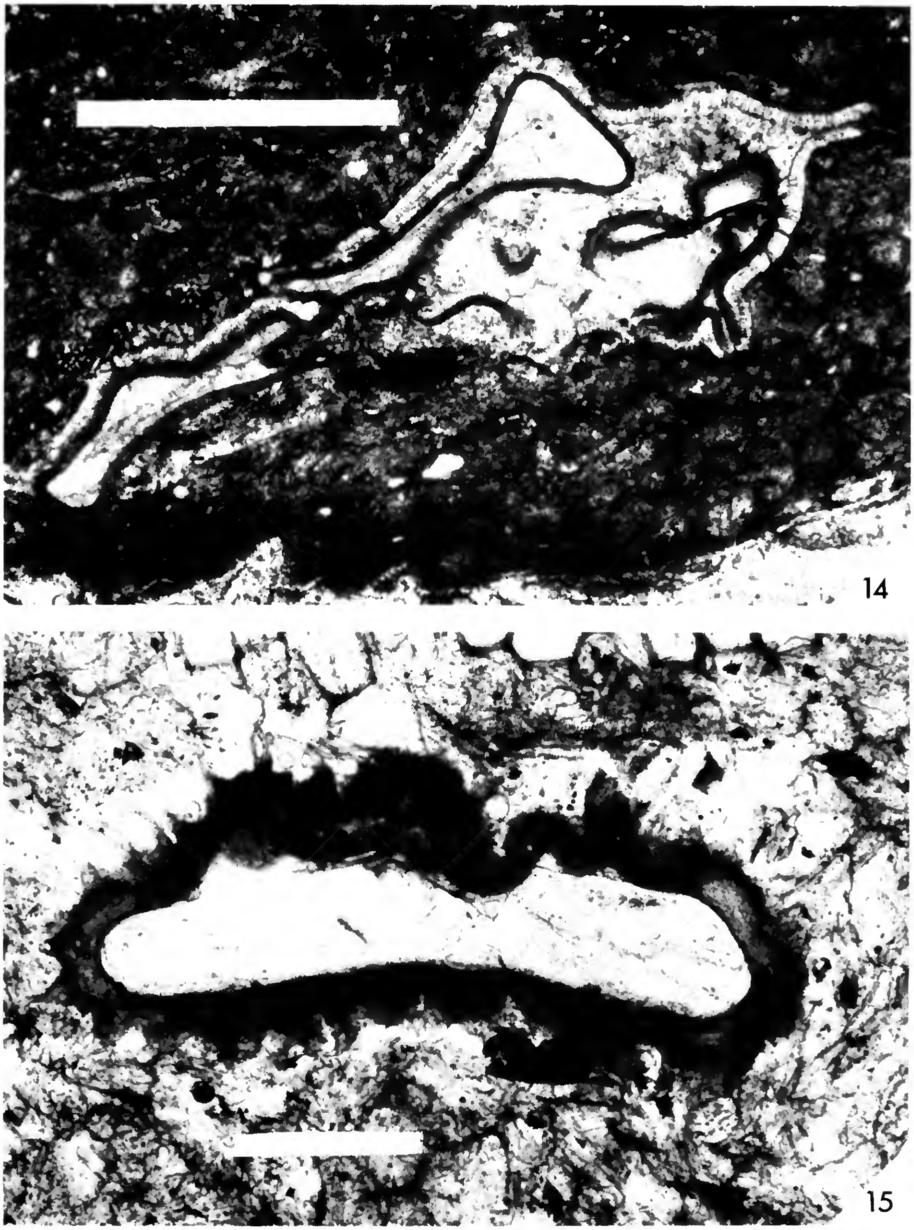


Fig. 13 *Anabathra pulcherrima* Witham. Transverse section of a fragment of outer cortex, closely associated with *A. pulcherrima* holotype. Note the secondary cortex (radially striated), the primary cortex of the leaf bases (stippled), some indication of leaf lamina retention (L), and an associated, free leaf lamina (F). Black shading represents destruction of cells by mineralization. V.62016. Scale bar represents 3·0 mm.

of the leaf bases are thick-walled and approximately isodiametric, about 30 μm to 50 μm across. Epidermal tissue is not preserved on the leaf bases, but the outermost tissue present is a hypodermis of thick-walled cells which lie parallel to the length of the leaf. No parichnos is visible in the available type material.

Isolated leaf laminae occur in the matrix sectioned in various planes (Fig. 11). In transverse section the leaves are rhomboidal, becoming triangular in section distally. Leaves vary from 1·5 mm to 2·5 mm in width, and are about 1·0 mm high. Leaf traces about 25 μm in diameter consist of up to ten tracheids, but there is a gap between the xylem and the innermost mesophyll. The mesophyll cells are thick-walled, closely packed, polyhedral, and up to 90 μm in diameter. The outermost preserved tissue is a continuous hypodermis, two to four cells thick, consisting of thick-walled cells arranged most numerously at the adaxial crest and abaxial keel of the leaf. Although no epidermis is preserved in the more intact leaves, a number of fragments of hypodermis probably originating from the same form of leaf occur in the matrix. These fragments sometimes show epidermal features such as stomata, but the preservation in this material is too poor for detailed description or illustration here.

Dispersed through most of the holotype sections of *A. pulcherrima* are several spiny megaspores (Fig. 15). From eleven such megaspores sectioned in several different planes, the range in equatorial diameter is 0·85 mm to 1·65 mm, with a mean value of 1·28 mm. The megaspores have a gula up to 50 μm tall and about 200 μm in width (Fig. 16). The exine varies between 15 μm and 35 μm in thickness, 20 μm being a typical value. Spines occur more densely on the distal surface where their bases may be only 40 μm apart. The spines are about 100 μm long, are slightly swollen at the base, but taper little along their length from a width of 14 μm. Spine apices are blunt. Nearer the gula, spines occur less densely, are generally shorter, and are usually reflexed. These features agree with the dispersed megaspores called *Lagenicula subpilosa* (Ibrahim) Potonié & Kremp, the rather large size of the spores falling within the range of the *major* form of the species (Dijkstra 1952). Among other *Lagenicula* species of similar age and geographical distribution, *L. horrida* Bennie & Kidston *ex* Zerndt (1934) and *L. crassiaculeata* Zerndt (1934) compare closely with these *in situ* megaspores. However, *L. horrida* has a more sparse covering of spines than has *L. subpilosa*; the spines of *L. horrida* taper progressively from their bulbous base to their pointed apex. The spines of *L. crassiaculeata* are of a similar surface density to those of *L. subpilosa*, but the longest exceed 180 μm; the gula of this species may be up to 800 μm in height. Chaloner (1953*a*) obtained *L. crassiaculeata* megaspores from the cone compression *Flemingites allantonensis* (Chaloner) Brack-Hanes & Thomas.



Figs 14–15 Megasporangium and megaspore associated with holotype of *Anabathra pulcherrima* Witham. Fig. 14, oblique section of megasporangium containing spores and showing prismatic cells of sporangium wall. Attributable to *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas. V.62012. Scale bar represents 1·0 mm. Fig. 15, oblique section of dispersed megaspore, attributable to *Lagenicula subpilosa* (Ibrahim) forma *major* (Dijkstra *ex* Chaloner) Potonié & Kremp. V.62015. Scale bar represents 240 μm.

In some instances, up to four megaspores have been sectioned still within the megasporangium (Figs 14 and 16). There is no evidence of abortive spores, but the size of the megasporangia indicates that they could have contained more than one tetrad of megaspores. The prismatic cells of the megasporangium wall are occasionally visible (Fig. 14). These cells are thin-walled, about 35 μm across radially and about 10 μm tangentially. No other cells are seen

within the intact megasporangia, and there are no microsporangia, sporophylls or intact cones in the available holotype material.

DISCUSSION. DiMichele (1980) emended the generic diagnosis of *Paralycopodites* Morey & Morey 1977, showing that what had first been considered a genus of herbaceous lycopsids were arborescent, lepidodendralean stems bearing deciduous, leafy, lateral branchlets. He specifically identified these stems from American Upper Carboniferous coal balls with material of *Lepidodendron brevifolium* Williamson from Pettycur, for which he designated a lectotype from that Scottish, Lower Carboniferous locality. DiMichele distinguished *Paralycopodites* from other lepidodendralean stem genera on such features as its persistent leaves, and its homogeneous outer primary cortex and periderm of thick-walled prosenchyma. As seen in transverse section, the smooth margin of the protostele differs from all known lepidodendralean steles except that of *Bothrodendron*, known only from Czechoslovakian and English coal balls (Williamson 1889; personal communication from Prof. K. V. Leistikow and Frl. Ulrike Bertram of Frankfurt). The deciduous, lateral branchlets are not peculiar to *Paralycopodites* since 'ulodendroid' scars which remain on the stem after these branchlets are abscissed are also known in *Lepidodendron*, *Bothrodendron* and *Lepidophloios* (Jonker 1976). Given that *P. brevifolius* is based upon a lectotype from the original material of Williamson, it is interesting that Williamson closely compared *L. brevifolium* to *A. pulcherrima* Witham. To quote Williamson (1872*a*: 227):

. . . we have, at once, the closest resemblance to WITHAM's *Anabathra* and CORDA's *Diploxylon*, as well as to those now under consideration. That WITHAM's plant is identical, in type, with mine, is further indicated by his tab. 8 fig. 12, where he exhibits one of the large compound medullary rays shown in my Plate XXVII fig. 23.

Similarly, Williamson (1872*b*: 310, footnote):

Until the very characteristic macrospores of my plant are shown to exist in some of the localities in which *Lepidodendron Veltheimianum* is common, I think it best to retain my proposed provisional name. I find these macrospores associated with a section of WITHAM's original specimen of *Anabathra pulcherrima*, for which I am indebted to Professor KING, and have not a doubt that the latter is identical with the Burntisland plant; but I have not sufficient proof to establish this point with the certainty requisite for a scientific determination.

From the description of the holotype of *A. pulcherrima* given above, there is clearly identity in xylem anatomy, and no essential differences in structure, between this species and the

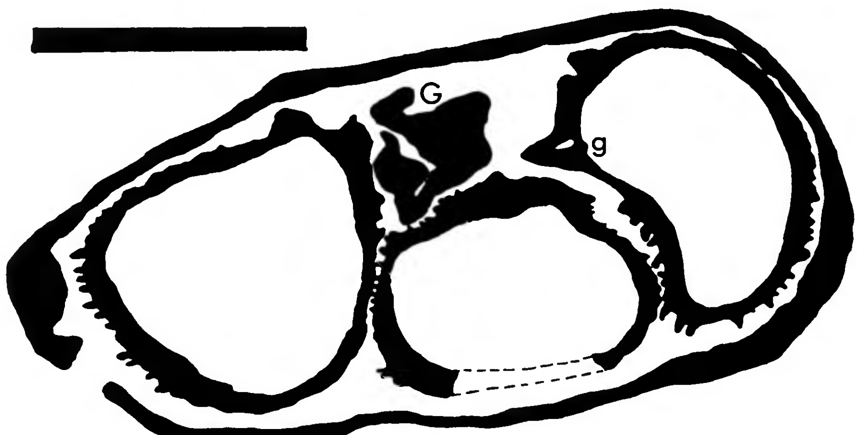
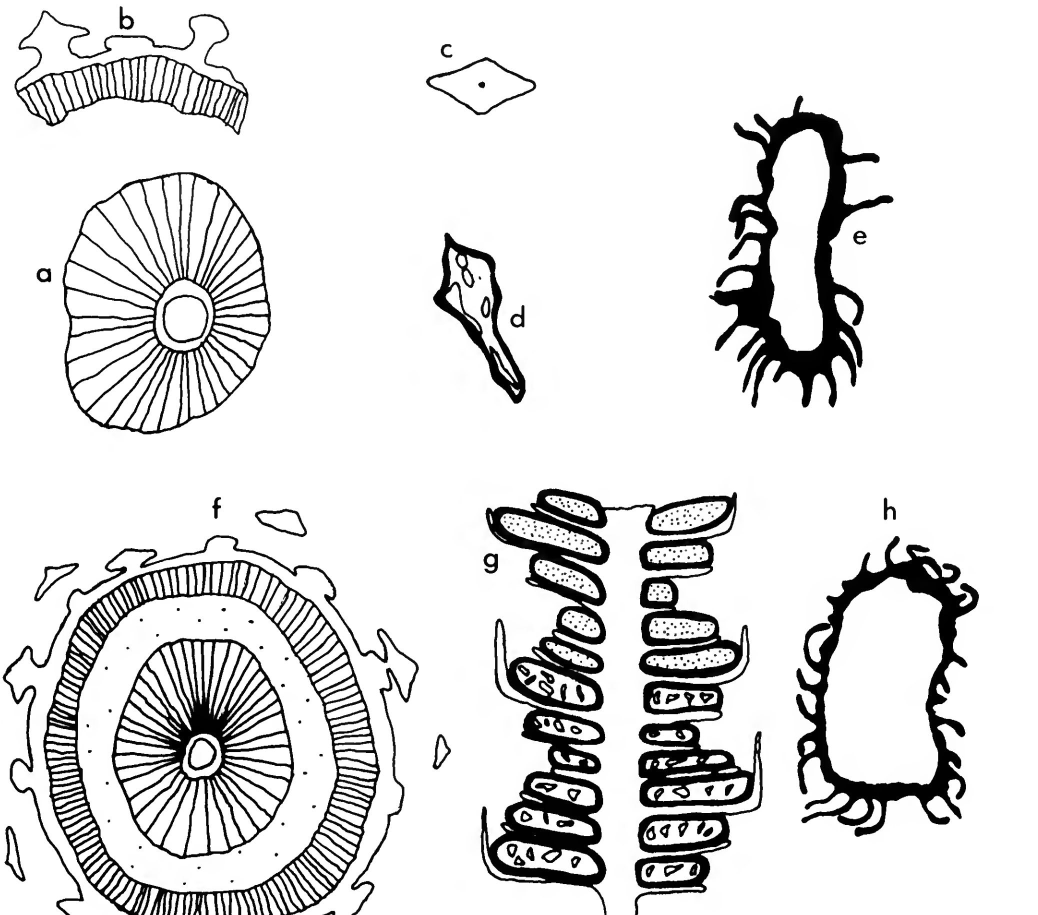


Fig. 16 Megasporangium associated with the holotype of *Anabathra pulcherrima* Witham. Oblique section, but probably close to tangential longitudinal plane of original, intact cone. Note apical gula structures of megaspores in transverse (G) and longitudinal (g) section. V.62018. Scale bar represents 1·0 mm.

material named *P. brevifolius*. Indirect evidence from the smaller stems with cortex, the secondary cortex with attached leaves, and isolated leaf laminae closely associated with the holotype of *A. pulcherrima* lend further support for the specific identification with *P. brevifolius*. Further, the megasporangia containing *Lagenicula subpilosa* associated with the holotype of *A. pulcherrima* are identical to the megasporangia of the cone *Flemingites scottii* associated with *P. brevifolius* at Pettycur. These structural comparisons between the various organs associated with *A. pulcherrima* at Allanbank and at Pettycur are summarized in Fig. 17.



Figs 17a–h Comparison of permineralized, Viséan lycopsid fossils from Allanbank, Berwickshire, with similar organs from Pettycur, Fife. Figs 17a–e, holotype of *Anabathra pulcherrima* Witham and associated organs from Allanbank. a, holotype stele in transverse section, × $\frac{2}{3}$; b, transverse section of outer cortex with leaves attached, × $\frac{2}{3}$; c, detached leaf lamina in transverse section, × 5; d, oblique section of megasporangium, × 10; e, oblique section of a megaspore referable to *Lagenicula subpilosa* (Ibrahim) forma *major* (Dijkstra *ex* Chaloner) Potonié & Kremp, ×40. Figs 17f–h, comparable lycopsids from Pettycur. f, transverse section of *Paralycopodites brevifolius* (Williamson) DiMichele, stem with attached and associated leaf laminae, × $\frac{2}{3}$; g, radial longitudinal section of part of *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas, bisporangiate cone, × 2·5; h, oblique section of a megaspore referable to *Lagenicula subpilosa* (Ibrahim) forma *major* (Dijkstra *ex* Chaloner) Potonié & Kremp, × 40.

Given the quality of preservation of the *A. pulcherrima* holotype, there is identity in structure between this and the lectotype of *P. brevifolius*. Under the International Code of Botanical Nomenclature (Voss 1983), Article 11.3 requires that *Anabathra pulcherrima* Witham take priority over *P. brevifolius*, and is the validly published and legitimate name for this fossil species.

Anabathra landsburgii (Kidston 1893), comb. nov.

1968 *Ulodendron landsburgii* (Kidston) Thomas: 425–428; figs A–D. (See this reference and Crookall (1964) for further synonymy, typification, locality, age, description, and remarks).

Emended diagnosis. Leaf bases greater in length than breadth. About 200 stomata/mm^2 on leaf bases.

Anabathra thomasiana sp. nov.

1967 *Ulodendron majus* Lindley & Hutton; Thomas: 778–779; figs 1, A–D. (See this reference and Crookall (1966) for further synonymy, locality, age, description and remarks, excluding *U. majus*, *sensu* Lindley & Hutton 1831 only.)

Diagnosis. Leaf bases greater in breadth than length. About 450–500 stomata/mm^2 on leaf bases.

Holotype. Specimen L.70, with eight slides of cuticle preparations made from it, of the Bradford Metropolitan Museums Service collection at Cliffe Castle Museum, Keighley, West Yorkshire.

Name. The epithet *thomasiana* is used here to commemorate the work of Dr Barry A. Thomas on the type of this species.

Comparison of *Anabathra* with *Ulodendron*

Lindley & Hutton (1831) established the name *Ulodendron* for stem compressions showing rounded, concave scars in longitudinal series, and with contiguous leaf bases in oblique rows. They named two species, *U. majus* and *U. minus*; Andrews (1955) designated *U. majus* as the type for the genus. Crookall (1966) and Jonker (1976) stated that the holotype material of *U. majus* Lindley & Hutton has apparently been lost, and a neotype specimen has been proposed by Crookall. The original description and figure of the *U. majus* holotype are not sufficiently detailed for other specimens to be readily identified with it. Indeed, Jonker demonstrated that the large scars on this holotype occur also on certain other lepidodendralean stem genera, and hence these scars alone do not serve to diagnose *Ulodendron* Lindley & Hutton as a distinct genus. Since its surface features differ in size only, *U. minus* is generally regarded as a synonym of *U. majus* (Crookall 1966). However, Jonker identified the neotype specimen of *U. majus* with *Lepidophloios laricinus* Sternberg 1825, thereby casting further doubt upon the generic distinction of *Ulodendron* Lindley & Hutton. As with the drawing and description of the lost holotype of *U. majus*, foliar details are very poor in the neotype specimen of that species, since it is in the form of an impression counterpart. Little would be gained by perpetuating the use of this confused and poorly typified generic name by applying it to specimens with evident 'ulodendroid' scars, but lacking in foliar detail.

Thomas (1967) described a compression specimen of the outer cortex of a stem on which linear leaf laminae were apparently still attached to rhomboidal leaf bases in oblique rows. He named this specimen *U. majus* Lindley & Hutton, and emended the diagnoses of the genus and species to include details of the leaves and cuticular preparations. This specimen differs from the holotype of *U. majus* in showing leaf laminae in close association, suggestive of organic connexion, and in having four distinct angles to the rhomboidal leaf bases. It is difficult to compare the features of the inner surface of detached cortex described by Thomas with the details of the external surface of the stem figured by Lindley & Hutton (1831: pl. 5). Thus, for example, it is not clear that the grooves between the leaf cushions described from the specimen

of Thomas compare with the apparently contiguous leaf bases or cushions shown by Lindley & Hutton. It is also uncertain from the holotype illustration of *U. majus* whether leaf laminae had been retained or shed. The emended diagnosis given by Thomas for *Ulodendron* could thus more usefully be applied to a new generic name encompassing *Ulodendron, sensu* Thomas 1967, *non* Lindley & Hutton 1831.

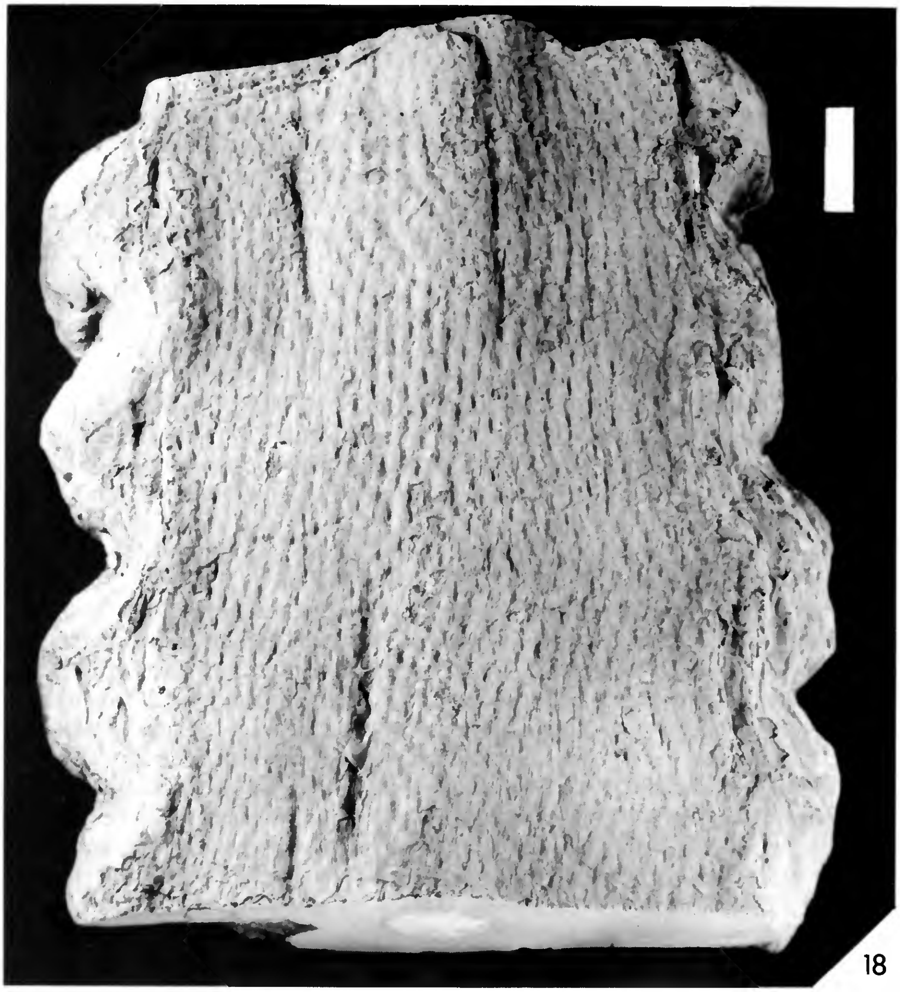
From the observations of Thomas, it is clear that the retention of leaf laminae on a stem large enough to show 'ulodendroid' scars distinguishes his specimen from all other described genera of lepidodendralean stem compressions. DiMichele (1980) compared *Ulodendron, sensu* Thomas, with the permineralized stem he called *Paralycopodites*, here regarded as a synonym of *Anabathra*. DiMichele did not unite these genera because he believed the anatomy of *Ulodendron* to be unknown.

Williamson (1872*a*) described a permineralized stem which he named *Ulodendron* on the basis of its lateral branch scars. The anatomy of the xylem and the cortex, and the broad leaf cushions bearing scars of foliar abscission seen in this specimen, indicate closer affinities with *Lepidophloios* than with *Ulodendron, sensu* Thomas.

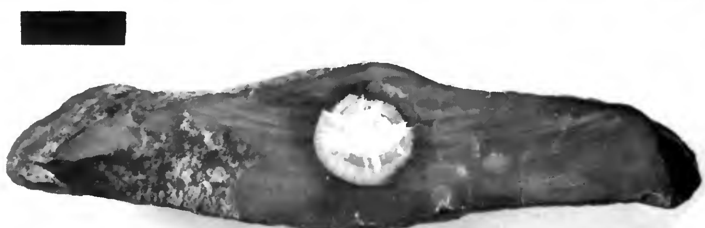
Carruthers (1869) briefly described an unusual but most significant specimen from the Westphalian of Yorkshire, now in the BM(NH) collections. (The parts of this specimen are registered under V.62037–41, with accompanying microscope slides. Two other '*Ulodendron*' specimens, V.282 and V.5987, show the same combination of modes of preservation. However, both of these retain very poorly preserved xylem, and only V.5987 yields cuticle.) This shows a permineralized xylem cylinder, a cortical cavity largely infilled with ferruginous shale, and a compressed, coaly surface (Figs 18, 18a). The specimen has two opposite rows of alternating, rounded, concave scars, and Carruthers used these features to identify it as *Ulodendron minus* Lindley & Hutton. The xylem has been preserved by a combination of calcite and pyritic permineralization, and peel sections were prepared from it. Exarch primary xylem forms what appears to have been a continuous cylinder in life (Fig. 19). From the approximately uniform thickness of the preserved primary xylem, it appears that the protostele was probably medullated in life. To one side of the oval protostele there is an outward bulge without evident disruption to the nearby secondary xylem, suggestive of unequal dichotomy of the stele. The metaxylem tracheids are polygonal in transverse section and vary between $100\,\mu m$ and $150\,\mu m$ in diameter. The protoxylem tracheids are arranged evenly and continuously around the outer margin of the primary xylem. The surrounding secondary xylem is generally more pyritized than the primary xylem, and so yields less anatomical detail. The radiating files of secondary tracheids are irregularly split into wedges, but no cellular structure can be seen in the intervening gaps. The secondary xylem tracheids are roundly rectangular in transverse section, and about $70\,\mu m$ in diameter. Radial and tangential longitudinal sections of the xylem were prepared, but pyritization has destroyed most of the cellular detail. However, from slide V.62040a it appears that the tracheids of both the primary and secondary xylem have scalariform wall thickenings, with minute fimbrils occasionally preserved between the transverse bars.

The coaly surface of this specimen has a finely striated appearance superimposed upon oblique rows of small protrusions, which represent the leaf bases. There are no indications of leaf scars as would be found on all other described genera of lepidodendralean stem compressions as well preserved as this. There is considerable variation across the coaly surface in the morphological detail observed, but in some areas there appear to be overlapping, linear laminae showing single, central midribs (Fig. 20). It is these laminae which give the specimen its finely striated appearance. Since some of the laminae taper, towards one end of the specimen only, and may appear in spiral arrangement, these structures are interpreted here as retained leaves. No leaf apices are visible. That these are surface features of a leafy stem is supported by the preparation of cuticular samples. Cuticles were obtained by oxidation of pieces of coaly matter with Schulze's solution, clearing in dilute ammonium hydroxide, washing in hydrofluoric acid, and mounting unstained in glycerine jelly.

There is considerable variation in the quality of epidermal anatomy visible in these cuticular preparations from the Carruthers specimen, and in many instances fine cracks hinder detailed observations. Thus, although no ligule pits were obtained, it cannot be concluded that this



18



18a

Figs 18–18a *Anabathra pulcherrima* Witham, emend. herein. Westphalian; Yorkshire. V.62037. Both scale bars represent 10·0 mm. Fig. 18, surface view of stem showing 'ulodendroid' scars of lateral branchlet abscission, and striated appearance due to persistent leaf laminae overlying spirally arranged leaf bases; coated with ammonium chloride. Fig. 18a, view of transverse section of same stem, showing permineralized xylem between coalified surfaces. The cortical cavity has been infilled with shale.

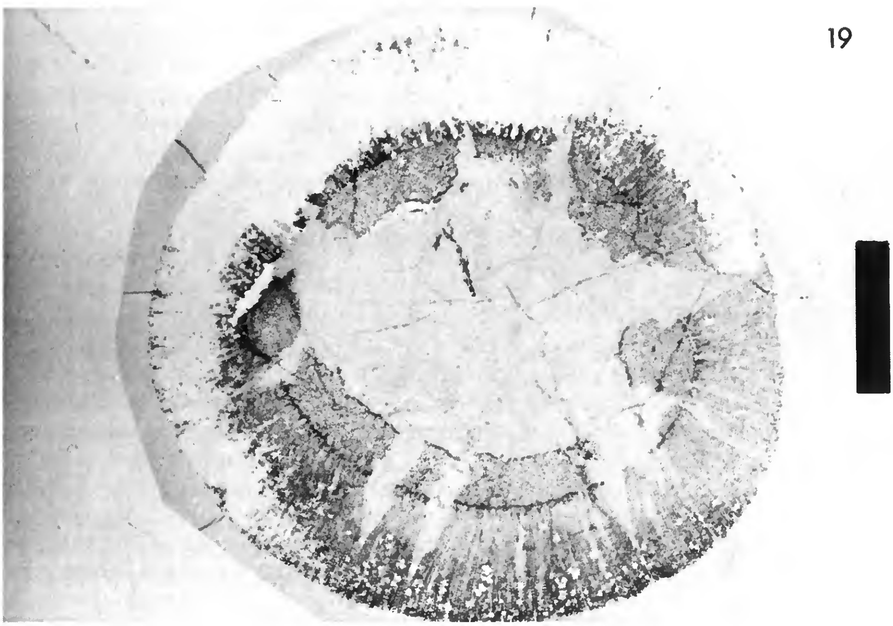


Fig. 19 *Anabathra pulcherrima* Witham, emend. herein. A peel of the permineralized xylem of specimen illustrated in Fig. 18. Note the central medullary cavity, and the smooth boundary between primary and secondary xylem. Pyritization of part of the outer, secondary xylem has destroyed much of the anatomical detail. V.62038a. Scale bar represents 5·0 mm.

plant was necessarily eligulate. A fragment of leaf base cuticle which does show certain details is shown in Fig. 21. The periclinal walls of the epidermal cells are flat and smooth. The anticlinal walls are straight or slightly curved, smooth, and about 1·5 μm to 2·0 μm thick. Stomata occur in apparently random orientation, and at a frequency of about 350 per mm^2. The cuticular

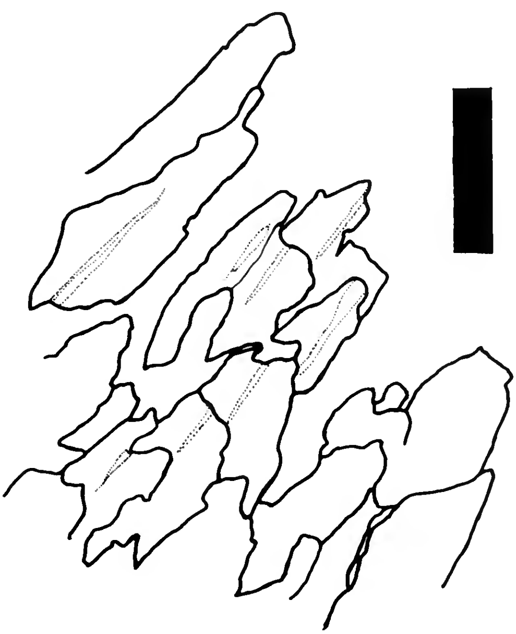


Fig. 20 *Anabathra pulcherrima* Witham, emend. herein. Detail of part of surface of specimen in Fig. 18. Note apparently truncated laminae, some with indications of a central midrib. Some of these slightly tapering laminae appear to be in oblique rows. V.62037. Scale bar represents 6·0 mm.

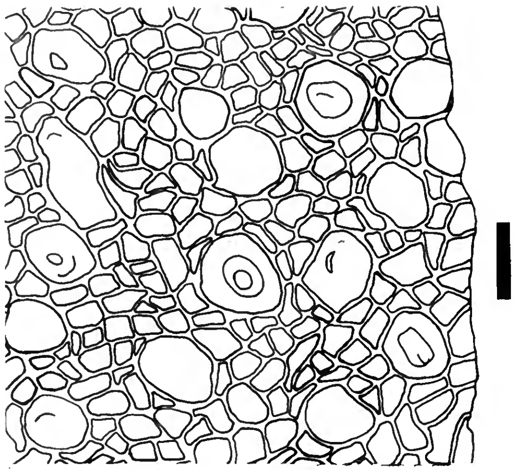


Fig. 21 *Anabathra pulcherrima* Witham, emend. herein. Detail of a cuticle preparation from a leaf base of specimen illustrated in Fig. 18. Note the stomatal pores, indistinctly separated guard cells, and abutting stomatal complexes. V.62037a. Scale bar represents 40 μm.

features of the guard cells appear in focus in the same plane as those of the other epidermal cells. The size and shape of the guard cells is variable, but most are about 40 μm long. Guard cells surrounding different pores are occasionally in direct contact with each other. There is no apparent longitudinal separation of the guard cells as seen from this cuticle. It seems unlikely that there was only one guard cell completely surrounding the stomatal pore, as in the Devonian psilopsid *Zosterophyllum* (Lele & Walton, 1961). All other known lycopsid stomata have two guard cells per pore. It is probable that the cuticle of the guard cells was thinner and no visible flange has been preserved at the junction of these cells. In some cases a rounded pore can be seen at the centre of the guard cells, surrounded by a zone of cuticle about 25 μm long and 15 μm broad. The stomatal pores have been preserved open, and this is evidently so in many of the stomata figured by Graham (1935) from several permineralized lepidodendralean leaves, including those of *A. pulcherrima* (his 'Type A'). The zone of cuticle immediately surrounding the pore shows no longitudinal division, in common with the remainder of the guard cell cuticle. Although clearly preserved in only a small number of stomatal structures, the features of the central pore and immediately surrounding zone of cuticle appear sufficiently regular such as not to have been much affected by degradation in the life of the plant, during its preservation, or by the preparation procedure. Possibly this zone and the pore were slightly sunken below the level of the remainder of the guard cell surface in life, but there is no great distinction of these levels as seen optically. Since some compression of the cuticle has occurred both vertically and obliquely, no detailed interpretation of the three-dimensional arrangement of cells around the stoma is offered here.

In all these cuticular features there are many similarities to the cuticles described as *U. majus* (Thomas 1967) and *U. landsburgii* (Thomas 1968). The size of the guard cells of the specimen described here compares more closely with *U. landsburgii*, but the stomatal frequency on its leaf bases is intermediate between that found in these two forms. Thomas (1966) concluded that, in general, lepidodendralean species can be distinguished using cuticular characters, but that generic delimitation of compression specimens still rests more on gross morphology. The external, megascopic details of the two *Ulodendron* species described by Thomas lend further support in correlating that genus with the Carruthers specimen (Fig. 18) described here. He described specimens of *U. majus* and *U. landsburgii* as having leaf laminae retained on quite large pieces of isolated cortex. As mentioned above, there is some difficulty in comparing the inner surface of cortical fragments with the outer surface of the specimen described here. These two named species of *Ulodendron*, *sensu* Thomas, are therefore here considered congeneric, but not conspecific, with *A. pulcherrina.*

The Carruthers specimen showing mixed preservation described here (Fig. 18) is identified as *Anabathra pulcherrima* Witham, since it compares closely with that species in xylem anatomy

and surface morphology, and differs from it in no visible features. The emended diagnoses given above retain *Anabathra landsburgii* (Kidston) comb. nov. and *A. thomasiana* sp. nov. as separate species on the basis of the shapes and stomatal frequencies of their leaf bases. From so few specimens, representing only the three species of *Anabathra* as yet recognized in the compression state, such diagnoses may well be provisional, our knowledge of the specific variations in size and form of both leaf bases and epidermal cells being so restricted. However, it seems preferable at present to retain these specific distinctions while awaiting further data.

The 'whole plant' of *Anabathra*

The name *Anabathra pulcherrima* as used here is taken to apply strictly to certain branching, leafy stems only. There is as yet no evidence for organic connexion between this specific organ and its reproductive or rooting structures. However, as has become common usage with more completely reassembled plants such as the '*Caytonia* plant' or the '*Cordaites* plant', the expression '*Anabathra* plant' seems the most appropriate for describing this lycopsid with its intact body reconstructed, the generic name of the stem being the oldest name given to any distinctive part of it.

DiMichele (1980) indicated the frequent association between *A. pulcherrima* and the bisporangiate cones now called *Flemingites* Carruthers in the permineralized state. In the Lower Carboniferous of Scotland, as mentioned above, one particular cone species associated with *A. pulcherrima* is *F. scottii.* Since it produces megaspores which would be attributable to *Lagenicula subpilosa* as a dispersed spore, this cone species differs from the cones *F. diversus* (Felix) Brack-Hanes & Thomas and *F. schopfii* (Brack) Brack-Hanes & Thomas, which are associated with *A. pulcherrima* in North American coal balls of Pennsylvanian (Upper Carboniferous) age. There are, of course, several other species of *Flemingites*, both compressions and permineralizations, which are not so closely associated with *A. pulcherrima.* Thus, permineralized cones from Roannais and Esnost in the Viséan of France (Galtier 1970), now referred to *Flemingites* sp., are associated with stems named *Lepidodendron rhodumnense* or *L. esnostense* at these localities rather than with *A. pulcherrima.* (However, the assignment of these stems to *Lepidodendron*, *sensu* DiMichele (1983), is debatable, and they may prove closer in generic affinity to *Anabathra*—see below).

Nothing is known directly of the rooting organ bearing the stem of *A. pulcherrima.* As mentioned above, no roots or rhizophores are preserved in the limestone at Allanbank. However, stigmarian rhizophores and rootlets are known from the Pettycur Limestone and these possibly formed the supporting rhizophores for *Anabathra.* Another lepidodendralean stem, *Lepidophloios scottii*, also occurs in the Pettycur Limestone, but because of its greater rarity at that site, it is unlikely that all the stigmarian axes belonged to *L. scottii* rather than to the much more abundant stems of *A. pulcherrima.* This point is of significance in the ordinal classification of *Anabathra* given below. (In certain coal ball floras dominated by *A. pulcherrima*, DiMichele has observed *Stigmaria* with *Anabathra*-like periderm—personal communication.)

Suprageneric taxonomy of *Anabathra*

One of the most widely accepted and used systems of classification for both fossil and living lycopsids is that proposed by Chaloner & Boureau (1967). Table 1 displays the main features used by these authors to characterize the lycopsid orders which they recognized; the '*A. pulcherrima* plant' as described above is included for comparison. Although there is some uncertainty over the form of rooting organ supporting the *A. pulcherrima* stem, it appears that this plant shows greatest similarity to the Lepidodendrales. The only character in which it differs from that order as represented in Table 1 is in its lack of scars of foliar abscission. Hence it seems reasonable to remove emphasis from foliar abscission as an apomorphy or distinctive feature for that lycopsid order, to allow the incorporation of the '*A. pulcherrima* plant'. This has, of course, been the ordinal designation already given to *A. pulcherrima* and *F. scottii* under their commonly used synonyms as species of *Lepidodendron* and *Lepidostrobus* respectively.

Table 1 Structural comparisons of '*Anabathra* plant' with orders of Lycopsida. + = presence of character, — = absence of character.

	Secondary growth	Leaf scars	Stigmarian rhizophore	Ligule	Leaf bases/ cushions	Heterospory	Cone
Drepanophycales	—	—	—	—	—	—	—
Protolepidodendrales	Rare	Rare	—	Rare	+	Rare	—
Lycopodiales	—	—	—	—	—	—	Some spp.
Miadesmiales	—	—(?)	—(?)	+	—	+	+
Selaginellales	Rare	—	—	+	—	+	Most spp.
Isoetales	+	—	—	+	—	+	—
Lepidodendrales	+	+	+	+	Most spp.	+	Most spp.
'*Anabathra* plant'	+	—	+(?)	+	+	+	+

Eight lepidodendralean families were proposed by Chaloner & Boureau, namely the Pleuromeiaceae, Bothrodendraceae, Cyclostigmaceae, Lepidodendraceae, Sigillariaceae, Lycopodiopsidaceae, Pinakodendraceae, and Lepidocarpaceae. Unfortunately, the characters used to diagnose these families include different organs according to the family in question. This has led to confusion when evidence for reconstruction has indicated, for example, that certain lepidodendracean stems probably bore cones of the Lepidocarpaceae (Thomas 1978). Ideally, the classification of these fossils would follow that of extant lycopsids in being based upon supposedly 'conservative' reproductive features, in conjunction with characters of attached or associated vegetative organs (Meyen 1975). However, with arborescent fossil plants such as the Lepidodendrales, fragmentation and separation of fertile and vegetative organs before preservation has made this procedure difficult or impossible for most specimens. For all but the Lepidocarpaceae, the type genera of lepidodendralean families are characterized by such features as foliar scars or leaf base morphology. The degree to which the circumscriptions of these essentially 'vegetative families' have been improved by evidence of connexion or association with reproductive structures is very variable. Thus, although sigillariacean stems are known to have borne the *Sigillariostrobus/Mazocarpon* form of cones, much less is known with certainty of how the Bothrodendraceae reproduced (Chaloner & Boureau 1967, Stubblefield & Rothwell 1981).

Since compression fossils of lepidodendralean genera are more common and diverse than the permineralized representatives, it is mainly from the surface morphology of *Anabathra* and the spore content of *Flemingites* that comparisons can be made with the established families of that order. The bisporangiate cones of *Flemingites* differ considerably from the separate mega- and microsporangiate cones of the Lepidocarpaceae and Sigillariaceae. In the Lycopodiopsidaceae and Pinakodendraceae the sporophylls are not aggregated to form cones. The Pleuromeiaceae include species which produced either mono- or bisporangiate cones. The Cyclostigmaceae and Lepidodendraceae are known to have produced bisporangiate cones, and this may have been so also for the Bothrodendraceae. However, foliar abscission leaving a leaf scar is characteristic of all stems at maturity in each of the lepidodendralean families so far recognized.

The lack of foliar scars due to leaf abscission in *Anabathra* should now be assessed for its relevance in familial taxonomy. Chaloner & Meyer-Berthaud (1983) proposed a model for the growth and abscission of lepidodendralean leaves in relation to stem growth and position of the leaves on the plant. They suggested that leaves were never abscissed from stems for which the ultimate diameter was less than about 10 mm. Such stems would obviously include lateral branchlets and the distal parts of any highly branched lepidodendralean crown. However, given isolated leafy shoots preserved as compressions lacking cuticle, there seems no way of assigning these fossils to particular genera, families or orders of lycopsids. (A comparable problem exists in the taxonomy of similar shoots of Carboniferous and Permian conifers. In that instance, specimens lacking in detail are assigned to the 'catch-all' genus *Walchia*, and a similar solution may be appropriate for small, detached, lycopsid leafy shoots.) Further problems arise when the maturity of the lepidodendralean shoot is considered. Kosanke (1979) has demonstrated that

lepidodendralean stems much larger than 10 mm in diameter can only rarely be found to have retained very long leaf laminae of the *Cyperites* form. Chaloner & Meyer-Berthaud suggest that such large, leafy stems represent shoots which were still juvenile; they had not yet produced a branching crown as they were still undergoing apoxogenetic development at the time of preservation (Eggert 1961). Given the presence of branchlets scars, shorter leaf laminae, and the greater abundance of leafy stems of *Anabathra* as here diagnosed, it appears that the retention of leaves by this genus on stems greater than about 10 mm is a feature of the plant at or near the completion of its determinate growth. This view is supported by the feasibility of preparation of cuticles from the leaf laminae of *A. thomasiana* (Thomas 1967) and *A. landsburgii* (Thomas 1968), while no such preparations have been obtained from the *Cyperites* form of lepidodendralean leaf. In general, leaves that are retained for longer periods have thicker, more resistant cuticles than caducous leaves.

It is on the basis of this kind of leaf lamina retention, in combination with the production of bisporangiate cones, that the lepidodenralean family Flemingitaceae is here recognized. The following is a list of genera which may be placed in the Flemingitaceae:

Flemingites Carruthers 1865, emend. Brack-Hanes & Thomas 1983 (Type genus).
Lagenicula Bennie & Kidston 1886, *ex* Zerndt 1934.
Lagenoisporites Potonié & Kremp 1954.
Lycospora Schopf, Wilson & Bentall 1944 (*pro parte*).
?*Stigmaria* Brongniart 1822 (*pro parte*).
Anabathra Witham 1833, emend. herein.
Brasilodendron Chaloner, Leistikow & Hill 1979.
Lepidodendron, *sensu lato*. (Those species where leaf laminae are retained on mature stems broader than about 10 mm.)

The monotypic genus *Brasilodendron*, Permian compressions of leafy stems from Brazil, is here assigned to the Flemingitaceae instead of to the Lycopodiopsidaceae as proposed by its authors (Chaloner, Leistikow & Hill 1979). Although no cones or fertile organs of any form are known attached to *Brasilodendron pedroanum*, megaspores named *Lagenoisporites brasiliensis* (Dijkstra) Trindade are intimately associated with these stems and probably represent the spores of the same plant. This genus of megaspores is known *in situ* only from *Flemingites* cones, and it seems probable that the *L. brasiliensis* megaspores came from such bisporangiate strobili rather than from the disaggregated sporophylls typical of the Lycopodiopsidaceae. Further, Chaloner, Leistikow & Hill (1979) compare *Brasilodendron* most closely to *Ulodendron*, *sensu* Thomas, in its retention of leaf laminae. They separated these two genera, however, on the basis of sigmoid leaf shape and absence of stomata on the leaf bases in *Brasilodendron*, features which also distinguish the latter from *Anabathra* as diagnosed here.

The genera *Lycospora*, *Stigmaria* and *Lepidodendron* are flemingitacean only in part, because their present diagnoses allow their inclusion in other lepidodendralean families also. Brack-Hanes & Thomas (1983) suggested that spores referrable to *Lycospora* from wholly microsporangiate cones (i.e. *Lepidostrobus* Brongniart, *sensu* Brack-Hanes & Thomas), have wider equatorial flanges or zonae than do the microspores of *Flemingites*. Further, these authors proposed that the *Lepidostrobus*-derived *Lycospora* show ornamentation on their proximal surfaces usually absent in the *Lycospora* from *Flemingites* spp. However, these differences between microspores do not serve to distinguish all species of the cone genera *Lepidostrobus* and *Flemingites* as Brack-Hanes & Thomas imply in their diagnoses. Thus, for example, Galtier (1970) has shown that the microspores of the Esnost *Flemingites* sp. have zonae as wide as those in the type specimen of *Lepidostrobus ornatus* Brongniart. Further, some of the bisporangiate cones included as species of *Flemingites* by Brack-Hanes & Thomas lack ligules (e.g. *F. brownii*), or do not contain the gula-bearing forms of megaspores (e.g. *F. brownii*, *F. gallowayi*, *F. noei*), and thus do not fall within their diagnosis for that genus of cones. If these particular species are to be retained within *Flemingites*, it would be more appropriate to concentrate on the bisporangiate nature of the whole cones rather than on the exact morphological details of the spores they contain.

Chaloner (1953*a*) correlated compressions of bisporangiate cones bearing megaspores referable to *Lagenicula horrida* and *Lagenoisporites rugosus* with the stem compressions named *Lepidodendron simile* and *L. acutum* respectively. (These cones are currently named *Flemingites gracilis* and *F. russellianus* respectively.) However, there is some uncertainty regarding the presence of leaf scars on these two species of *Lepidodendron* (Crookall 1964). Although given this generic designation by Nemejc (1947), these two stem species are known as leafy shoots lacking distinct foliar scars, and with no anatomical or cuticular details. Many of the shoots are not large enough to have shed their leaf laminae to show the leaf cushion details characteristic of *Lepidodendron* Sternberg *sensu stricto.* Similar problems can be found amongst permineralized material, such as with *Lepidodendron rhodumnense* and *L. esnostense* from the Viséan of France. Thus, such leafy shoots might be equally referable to a number of lycopsid orders and genera, such as *Lycopodites*, *Lepidophloios* or *Anabathra* as diagnosed here. Moreover, certain stems assigned to *Lepidodendron* are known both in organic connexion and in frequent association with cones of the lepidocarpacean *Achlamydocarpon* (Leisman & Rivers 1974, DiMichele 1979, 1983). In this way, stems of the Lepidodendraceae are being attributed to the Lepidocarpaceae or Flemingitaceae.

As discussed above, *Stigmaria* is in part classified under the Flemingitaceae, as being the probable rhizophore for this along with all the other lepidodendralean families, but the evidence for its inclusion is only circumstantial.

In the megasporangiate cone *Caudatocorpus* Brack-Hanes (1981), both the abortive and functional spores have been assigned to *Lagenicula.* However, this genus of cones seems to be more closely allied to the Lepidocarpaceae than to the Flemingitaceae, since it contains only one functional spore per megasporangium, and the cones were not bisporangiate.

As DiMichele (1980) has commented, it is interesting that although associated with different species of *Flemingites* cones, the permineralized stems of *Anabathra* found in Europe and North America from the early Viséan to the end of the Westphalian (or their American equivalents) vary so little in their anatomy that all have been included in the single species *A. pulcherrima.* The same apparent stability in vegetative structure may be seen for a comparable stratigraphic range in the probable rhizophore of these and other lepidodendralean plants, *Stigmaria ficoides.* From the list of flemingitacean genera given above, the stratigraphical ranges for the megascopic and microscopic genera show only partial coincidence. Thus, although all these genera except *Brasilodendron* are known from the Viséan to the Westphalian, *Lycospora*, *Lagenicula* and *Lagenoisporites* have been recorded also from the Devonian (Chaloner 1967). In part, this reflects the greater likelihood of a plant to be preserved as its very numerous and highly resistant spores rather than as its fewer, more fragile and degradable larger organs. These two megaspore genera have no known affinities other than with bisporangiate cones, whereas *Lycospora* is known also from purely microsporangiate cones. Thus, although megafossil evidence is lacking, palynology suggests that the Flemingitaceae may have first occurred in the Upper Devonian.

Preservation and nomenclature of fossil plants

Although a variety of modes of preservation have been recognized (Schopf 1975), and rare combinations or intermediates between these modes found, most fossil vascular plants are known either as compressions/impressions or as permineralizations. These forms of fossilization result from rather different sets of physical and chemical processes, but a given plant organ is obviously susceptible to either. Correlations can be looked for between permineralized and compressed states of an organ by making comparisons such as those based on the following.

Spore or pollen grain contents. Thus, for example, Chaloner (1953*b*) found that megaspores belonging to the dispersed spore genus *Tuberculatisporites* occur in cones preserved both as compressions, *Sigillariostrobus*, and as permineralizations, *Mazocarpon.* This approach has some value in correlating vegetative organs indirectly. For example, certain leafy stems are

correlated above by their association or organic connexion with cones of *Flemingites*, both in the compressed and permineralized states.

Geographical and stratigraphical ranges. There is, of course, considerable variation in how widely given taxa of fossil plants occur through time and space. Provinciality in vascular floras is particularly evident between the continents of Upper Carboniferous and Permian times. However, the restricted ranges of fossil plants tend to be used more to deny correlations than to give positive identifications. Thus, taeniopterid leaf impressions from the Pennsylvanian (Upper Carboniferous) of North America are unlikely to belong to the Pentoxylales since that order is restricted to the Jurassic of India, Australia and New Zealand.

Superficial features. The scale of details used to compare the surfaces of compressed and permineralized organs ranges from gross morphology to that of epidermal anatomy obtained from cuticles and paradermal sections. *Sphenopteris hoeninghausii* provides an example where pinnule morphology, the presence of glandular hairs, and the 'dictyoxylon' cortex seen in partially decorticated stem compressions can be compared very closely to, if not specifically identified with, the permineralization *Lyginopteris oldhamia* and its associated organs (Scott 1923). It is, of course, more difficult to compare the microscopic details of epidermal anatomy between these preservation states. Many compressions lack cuticles, and even where cuticle is well preserved, it may have been compressed in such a way that direct comparison of cellular details with a permineralized epidermis is restricted. Correlations between leaf cushion features of permineralized and compressed Lepidodendrales have been made for certain species of, for example, *Sigillaria* (Chaloner & Boureau 1967) and *Lepidodendron* (DiMichele 1983).

Organic connexion between permineralized and compressed tissues. As mentioned above, such a combination of preservation states within one specimen is very rare, but an example can be found in the Devonian progymnosperm *Archaeopteris/Callixylon* (Beck 1960). Organic connexion provides, of course, the strongest unequivocal evidence for correlating organs between preservation states, but it is nevertheless dependent upon the quality of preservation.

This list of methods for correlating permineralizations with compressions may not be exhaustive, but it is evident that there are many limitations to the procedures. One great difficulty arises from the use of diagnostic characters for a genus or species that can only be observed in permineralizations. Thus, Benson (1918) emphasized the presence of a subarchesporial pad of parenchyma in the diagnosis of the permineralized cone *Mazocarpon*. In spite of the same form of spores occurring in the compressed cone *Sigillariostrobus* as in *Mazocarpon*, their overlapping stratigraphical and geographical ranges, their similar surface morphologies, and the association of each with stems of *Sigillaria*, the two generic names for these cones have not been strictly synonymized because the parenchymatous pad has not been preserved in the compressions.

Each of the four approaches to correlation outlined above has been used to some degree in comparing *Anabathra* with *Ulodendron*, *sensu* Thomas. None of the first three lines of evidence, taken individually or in combination, would probably provide sufficient evidence for an unequivocal identification of these two generic concepts with each other. However, notwithstanding the quality of preservation, the evidence provided by organic connexion in V.62037 (Fig. 18) surely brings these two genera together.

Classification and nomenclature are two distinct but interacting fields (Jeffrey 1976). Ideally, observations on and opinions about unnamed specimens could produce a classification which would then require the application of names for the chosen taxa. In practice, of course, our knowledge and understanding of fossil plant structure has been in a continuous state of change from the beginning of palaeobotanical studies, and this is reflected in changing taxonomy. In this paper, new lines of evidence are presented strengthening the comparison of *Anabathra* to *Ulodendron*. From the discussion above, it is clear what specimens fall within *Ulodendron*, *sensu* Thomas 1967, but it is debatable whether that sense is the same as *Ulodendron* of Lindley & Hutton 1831, or of other authors. Expressing my own opinion, therefore, *Ulodendron*, *sensu* Thomas, is here regarded as a synonym of *Anabathra* in its emended sense.

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Meyenodendron borealis gen. et sp. nov., a new lepidodendrid of angaran affinity from northern Alaska

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Synopsis

Several angaran lepidodendrids are reported from the Brooks Range, Alaska. One specimen, putatively from the Kuna Formation of the Lisburne Group, shares the characters of both *Tomiodendron* Radczenko and *Angarophloios* Meyen. This specimen is described and named *Meyenodendron borealis* gen. et sp. nov. A similar specimen from the Lower Namurian of north-eastern U.S.S.R. is named *Meyenodendron sibirica.*

Introduction

Meyen (1976), in his paper on angaran Carboniferous and Permian lepidophytes, redefined both *Tomiodendron* Radczenko and *Angarophloios* Meyen. *Tomiodendron* has elongated, oval, rhomboid or sagittal leaf cushions with persistent leaves and is ligulate. *Angarophloios* has obovate, oval or rhomboidal leaf cushions with rounded corners and infrafoliar bladders. Its leaves are persistent but there is no evidence of ligule pits in the axils of the leaves. The same distinction between the two genera is maintained in the key of lycophytes given by Thomas & Meyen (1984).

A single specimen was also figured by Meyen (1976: text-fig. 25; pl. 11, fig. 84) that combined characters of *Tomiodendron* and *Angarophloios.* Its leaf cushions show both ligule pit casts, as in *Tomiodendron*, and infrafoliar bladders, as in *Angarophloios.* The extended lower angles of the leaf cushions are more like those of *Tomiodendron.* Meyen did not refer the specimen to either genus and did not attempt to give it a name. A further specimen has since been found in Alaska showing the same combination of characters of the two genera. It allows us to both re-evaluate the taxonomic position of such intermediate forms and to comment on their geographical distribution.

Material

The new specimen came from the Kurupa Hills region of the Brooks Range in northern Alaska: lat. 68° 22′ 44″ N, long. 154° 48′ 20″ W (Fig. 1). It was found as a 'float' by Jerry Siok (University of Alaska) and appears to have come from a black chert horizon in the Kuna Formation of the predominantly marine Lisburne Group. Radiolaria and conodonts from the chert have generally been dated as Meramecian and Chesterian (personal communication C. G. Mull, 1984). This is equivalent to late Viséan to middle Namurian.

The specimen has been deposited in the British Museum (Natural History), London (register no. V.62164).

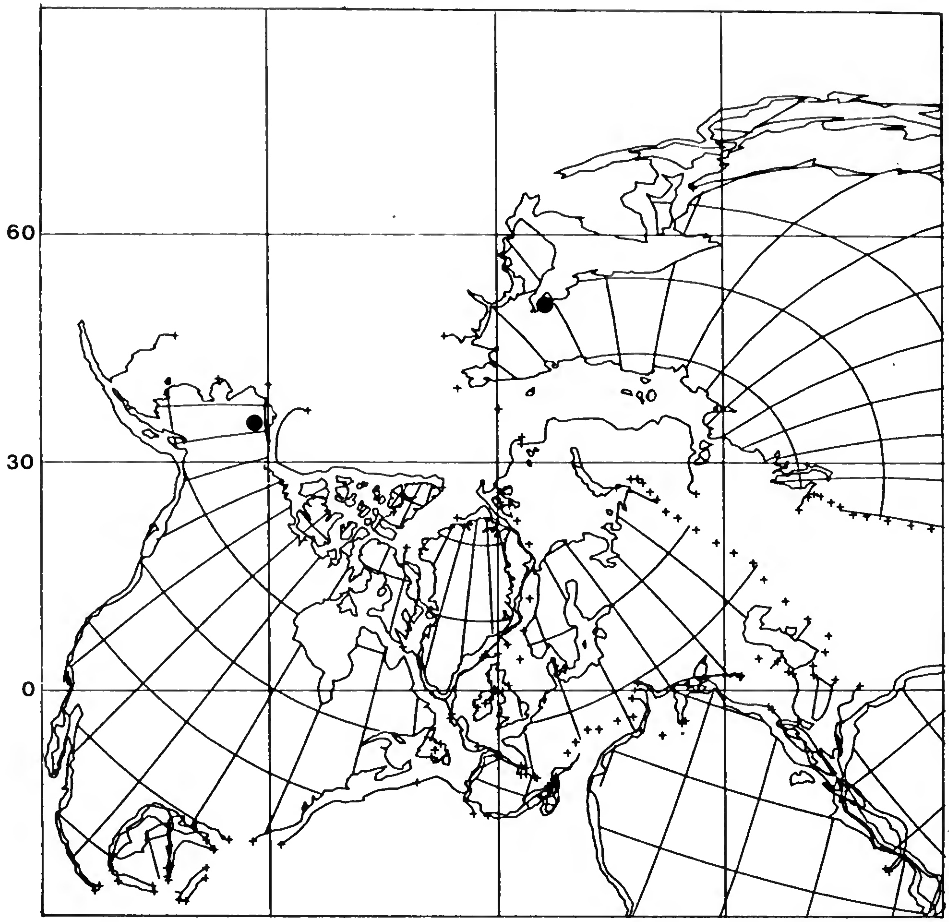


Fig. 1 Palaeocontinental reconstruction for the Namurian showing the relative positions of Alaska and Siberia. Solid circles indicate *Meyenodendron* localities. After Smith, Hurley & Briden (1981), map C.

Systematic descriptions

Division **LYCOPHYTA**

Order **PROTOLEPIDODENDRALES**

Family **PROTOLEPIDODENDRACEAE** (satellite taxon)

MEYENODENDRON gen. nov.

DIAGNOSIS. Leaf cushions with distinct outlines, obovate with rounded upper and side angles. Phyllotaxy lepidodendroid. Leaves persistent, attached to upper angle of the leaf cushion. Infrafoliar bladder in the upper half of the cushion. Ligule pits in the upper angles of the leaf cushions.

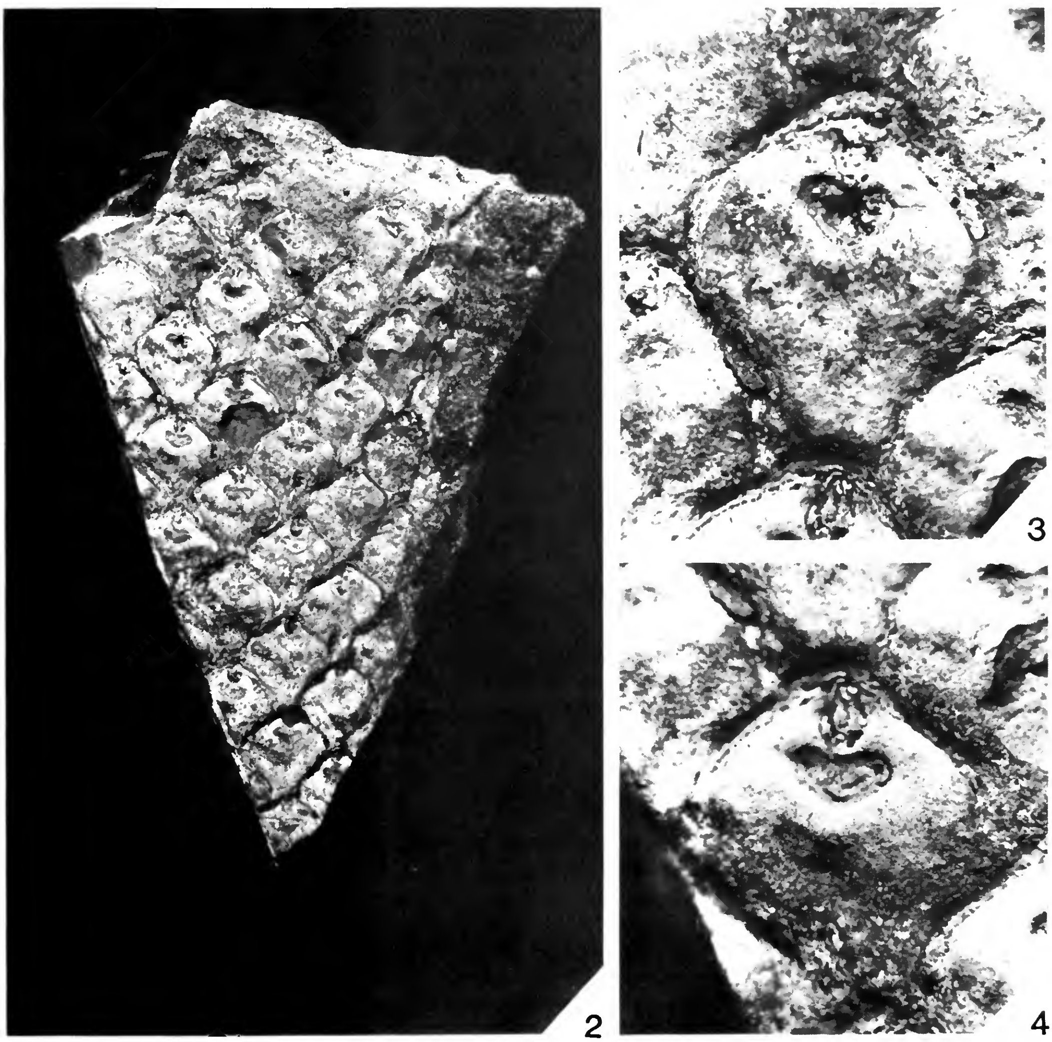
TYPE SPECIES. *Meyenodendron borealis* sp. nov.

NAME. For S. V. Meyen.

DESCRIPTION. The single specimen shows a small area of stem surface, well preserved as a cast with raised leaf cushions in two opposed parastiches at an angle of about 86° to each other. The cushions are all about 13 mm long and 10·5 mm broad, with rounded upper and lateral

angles. Laterally elongated and somewhat heart-shaped depressions, which we equate with Meyen's infrafoliar bladders, are present in the upper halves of the leaf cushions. A ligule pit cast is also clearly visible in the upper angle of each leaf cushion. The best preserved of these are flask-shaped and attached to remnants of coal running around the upper angles of the leaf cushions. The thickening of this coal into a triangular 'cap' to the cushion probably represents the broken base of the leaf lamina which was lost when the rock was split to expose the cushions. Unfortunately, no organic residue was preserved on any of the leaf cushions so no cuticle could be prepared.

COMPARISON. The possession by leaf cushions of both a ligule pit and an infrafoliar bladder poses a problem, for these two features have previously been used as major characters for generic distinction. *Tomiodendron* and *Angarophloios*, as defined by Meyen (1976), are clear and understandable genera based on leaf cushion characters. Meyen's use of *Tomiodendron* has been followed by Thomas & Purdy (1982). De Rouvre (1984), however, has described some



Figs 2–4 *Meyenodendron borealis* gen. et sp. nov. Fig. 2, **holotype** V.62164, × 1. Fig. 3, leaf cushion of same showing infrafoliar bladder, × 4. Fig. 4, leaf cushion of same with ligule pit and infrafoliar bladder, × 4.

rather different Lower Carboniferous lycophytes from Niger as *Tomiodendron varium*. They are described and drawn as having parichnos on their cushions, although the parichnos cannot be seen in the photographs.

It seems to us neither desirable nor practical to blur the definition of either *Tomiodendron* or *Angarophloios* by including intermediates. Neither does it seem sensible to merge the two. Therefore we propose to erect the new genus *Meyenodendron*, and include it in the list of satellite taxa of Protolepidodendrales outlined by Thomas & Brack-Hanes (1984). There are, however, sufficient differences between the two known specimens to prevent us believing them to be conspecific. The shapes and sizes of the ligule pits and infrafoliar bladders of the two show the same magnitude of differences as are used to distinguish other species of angaran lycophytes. We therefore prefer to create two species, even though only one specimen is known of each.

Meyenodendron borealis sp. nov.
Figs 2–5

Diagnosis. Leaf cushions 13 mm long, 10·5 mm broad. Infrafoliar bladders broadly cordate, central, 2 mm long, 4 mm broad. Ligule pit casts flask-shaped, 2 mm long, 1·5 mm broad at base.

Name. 'Northern'.

Holotype. No V.62164, British Museum (Natural History), London. Figs 2–5.

Locality. Collected as 'float' in Kurupa Hills, Brooks Range, Alaska.

Stratigraphy. Not *in situ*. Possibly Meramecian to Chesterian: Viséan to Namurian.

Meyenodendron sibirica sp. nov.

1976 Lepidophyte, incertae sedis; Meyen: text-fig. 25; pl. 11, fig. 84.

Diagnosis. Leaf cushions 25 mm long, 15 mm broad. Infrafoliar bladders oval, 5 mm long, 4 mm broad. Ligule pits very small, about 1 mm long.

Name. 'Siberian'.

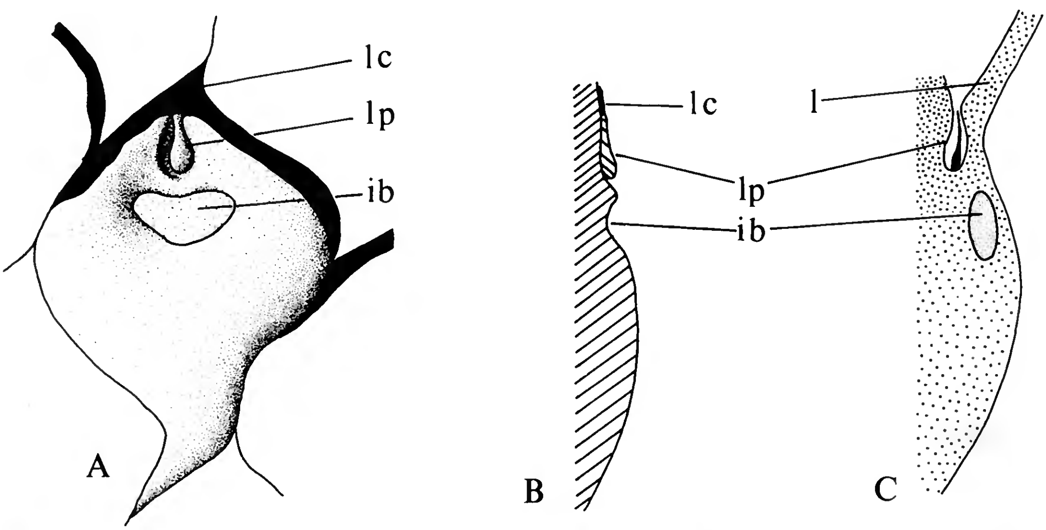


Fig. 5 *Meyenodendron borealis* gen. et sp. nov. **Holotype**, V.62164. A, leaf cushion as seen in surface view. B, median longitudinal section through a compressed leaf cushion as illustrated in A. C, reconstructed median longitudinal section through a leaf cushion as in life. (ib, infrafoliar bladder; l, leaf lamina; lc, leaf lamina compression; lp, ligule pit—with ligule in C).

HOLOTYPE. No 3791/156, Geological Institute, Academy of Sciences, Moscow.

LOCALITY. Paren River, left bank, 1·3 km below mouth of the Belye Snegi Creek, north-east of the Soviet Union.

STRATIGRAPHY. Khayamska suite, Serpukhovian stage (Lower Namurian).

Discussion

The discovery in northern Alaska of a lycophyte that can be put into the same genus as one from north-eastern Siberia is very exciting. The Alaskan specimen is well preserved and the surface of the impression shows little sign of abrasion. We assume from this that the stem was not transported for any appreciable distance before it was fossilized. Unfortunately the fact that the specimen was not found *in situ* makes any assessment of the depositional environment meaningless. Any palaeogeographic interpretations based on a single such specimen might be regarded with suspicion, although other lepidodendrids of American affinity have also been collected recently from the Kurupa Hills. These, attributed by us to *Tomiodendron varium* (Radczenko) Meyen, *Ursodendron chacassicum* Radczenko and *Angarophloios* cf. *leclerqianus* Meyen, were all found *in situ* in units stratigraphically underlying that which probably yielded the *Meyenodendron*. They therefore correlate with Russian material of Tournasian to Viséan age.

It therefore seems that, during the early Carboniferous, northern Alaska and north-eastern Siberia had floral elements in common which are not found in Europe. From the evidence of such floral similarities it can be argued that these areas were in much closer proximity to one another at that time. This conclusion is contrary to some widely used palaeocontinental reconstructions (e.g. Smith *et al.*, 1981; see Fig. 1). Further studies of Alaskan Carboniferous floras are certainly needed if we are to obtain a clearer picture of the late Palaeozoic palaeogeography of the areas.

Acknowledgements

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